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HUMAN PHYSIOLOGY.

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HENRY C. LEA.
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A TREATISE

L. M. F. Wanzer

1875—

ON

HUMAN PHYSIOLOGY;

DESIGNED FOR THE USE OF

STUDENTS AND PRACTITIONERS OF MEDICINE.

BY

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SIXTH EDITION,

REVISED AND ENLARGED.

WITH

THREE HUNDRED AND SIXTEEN ILLUSTRATIONS.

PHILADELPHIA:
HENRY C. LEA.
1875.

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PHILADELPHIA:
COLLINS, PRINTER,
705 Jayne Street.

TO MY FATHER,

JOHN C. DALTON, M.D.,

IN

HOMAGE OF HIS LONG AND SUCCESSFUL DEVOTION

TO THE

SCIENCE AND ART OF MEDICINE,

AND IN

GRATEFUL RECOLLECTION OF HIS PROFESSIONAL PRECEPTS AND EXAMPLE,

This Volume

IS RESPECTFULLY AND AFFECTIONATELY

INSCRIBED.

PREFACE.

In the present edition of this book, while every part has received a careful revision, the original plan of arrangement has been changed only so far as was necessary for the introduction of new material. Although the whole field of physiology has been cultivated, of late years, with unusual industry and success, perhaps the most important advances have been made in the two departments of Physiological Chemistry and the Nervous System. The number and classification of the proximate principles, more especially, and their relation to each other in the process of nutrition, have become, in many respects, better understood than formerly; though it is evident that this fundamental part of physiology is to receive, in the future, modifications and additions of the most valuable kind.

In nearly every division of physiological study, a prominent feature of recent progress has been the increased attention paid to quantitative investigation. The conviction has apparently become general that, in physiology as well as in other natural sciences, the knowledge gained by any method of study is essentially imperfect until its results can be stated in figures. The chemical characters of an ingredient or product of the animal system are hardly more important than its quantity; and for determining its physiological relation to other substances, of similar or different kinds, the knowledge of its quantity is absolutely indispensable. Investigations of this sort, in respect to the living body, are surrounded with difficulties; but the results obtained are steadily increasing in precision and extent, and already form a most important element in the study of physiology.

In a text-book like the present, it is desirable that the reader should not be misled by having all the frequent changes of opinion, or substitutions of theory, presented as discoveries in physiological science. Any faithfully observed facts, however unexpected or peculiar, are of course at once invested with a permanent value. But the theoretical explanations, by which they are sometimes accompanied, are not of the same importance. They often represent only a scheme of probabilities

existing in the mind of the author, and may be altered at any time to suit the requirements of more extended observation. In rendering an account, therefore, of the state of knowledge upon any physiological subject, the student should be informed, not only of the results now in our possession, but also of the means of investigation by which they have been attained. He is thus enabled to distinguish between what is positive in physiological doctrines, and what is hypothetical; and when further discoveries are made, which lead to changes of opinion, he is not confused or disappointed at apparent contradictions between the new views and the old. This method requires a certain amount of detail in the statement of facts; but its advantages are ample compensation for the necessary expenditure of time and space.

The additions and alterations in the text, requisite to present concisely the growth of positive physiological knowledge, have resulted, in spite of the author's earnest efforts at condensation, in an increase of fully fifty per cent. in the matter of the work. A change, however, in the typographical arrangement has accommodated these additions without undue enlargement in the bulk of the volume.

The new chemical notation and nomenclature are introduced into the present edition, as having now so generally taken the place of the old, that no confusion need result from the change. The centigrade system of measurements for length, volume, and weight, is also adopted, these measurements being at present almost universally employed in original physiological investigations and their published accounts. Temperatures are given in degrees of the centigrade scale, usually accompanied by the corresponding degrees of Fahrenheit's scale, inclosed in brackets.

NEW YORK, September, 1875.

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HUMAN PHYSIOLOGY.

INTRODUCTION.

THE study of Physiology embraces all the active phenomena presented by living beings—such as growth, reproduction, movement, sensation, the chemical changes manifested in the body during life, as well as its action upon external substances and its dependence upon external conditions.

Living bodies are distinguished, as regards their structure, from those of the inorganic world mainly by the fact that they are *organized ;* that is, they are composed of a number of different parts, or organs, connected with each other and mutually dependent. In all the higher orders, both of animals and plants, these various organs belonging to the same body are quite numerous, and are very different from each other both in their structure and properties.

In an animal, for example, there is an external integument covering the surface of the body, bones which form a framework for the protection and attachment of other parts, muscles by which the limbs are put in motion, an alimentary canal for the digestion of the food, and various glands for the secretion of the animal fluids. In a plant there are roots which absorb the ingredients of the soil, leaves which elaborate the vegetable juices, and the various parts of the blossom which are concerned in the production of the fruit. Thus each different organ has a special structure, and plays a distinct part in the living organism.

The peculiar action or result accomplished in this way by a particular organ is called its *function.* There are, therefore, a variety of functions going on in the living body, each one as distinct as the organ by which it is performed. But no one of them is entirely independent of the rest. The circulation of the blood, which is carried on by the organs of the vascular system, requires that the blood should be incessantly renovated by the process of respiration in order that it may continue undisturbed; and the circulation is in its turn necessary to the functions of secretion and nutrition, for which it supplies the necessary material to all parts of the body. Thus all the different functions are in a state of mutual dependence, and the life of the whole body is a result of the simultaneous and harmonious action of its different parts.

The only method by which physiology can be studied is the observation of nature. The phenomena presented by living creatures are only to be learned by direct examination, and cannot be inferred, by any process of reasoning, from any other facts of a different character. Even a knowledge of the minute structure of a part, however exact, cannot furnish any information as to its active properties or function; and these properties can be learned only by examining the organ when it is in a state of activity. Thus the muscular fibre and the nervous fibre present certain well-defined characters of minute structure which are easily distinguished by anatomical examination, but which could not teach us anything of their physiological properties; while direct experiment shows that the muscular fibre is contractile and the nervous fibre excitable or sensitive.

Since the vital phenomena of the entire body result from the combined activity of its different parts, these different parts should be studied by themselves in order to ascertain their particular properties. This can be done by examination and experiment for each part while it still retains its vital powers. Experience shows that after the circulation has ceased, and consciousness and volition have disappeared, many minute portions of the body continue for a time capable of manifesting their physiological action. Thus a muscular fibre, separated from the remaining tissues, may still be made to contract under the appropriate stimulus; and a nerve, though cut off from its connection with the brain, may also be called into activity by mechanical or electrical irritation. This is because each part retains its physiological powers so long as it retains its peculiar structure and constitution. The general functions of the body, such as the circulation, digestion, and respiration, have for their object to provide for the nutrition of the tissues and organs, and thus maintain their natural constitution unimpaired. Their cessation, accordingly, does not instantly destroy the vitality of particular parts, but only after a sufficient time has elapsed to alter or impair their natural constitution. The time during which the vital powers may thus be retained varies for different parts. Thus the muscular fibre is capable of manifesting its excitability, as a general rule, longer than the nervous fibre, and the nervous fibre longer than the gray matter of a nervous ganglion. There is, also, a difference in the same part shown by different kinds of animals. The excitability of both nervous and muscular tissues continues longer in the cold-blooded than in the warm-blooded animals, and in the quadrupeds longer than in birds. In every instance, of course, the examination of such an isolated part of the body should be made while it still preserves its physiological properties.

On the other hand, the functions of entire organs, or the general functions of the body as a whole, can only be studied with success while life is going on. The anatomical relations of the various organs may be learned by dissection after death; but their vital actions are not to be ascertained in this way, because they have ceased and cannot

again be put in operation. The most important facts have often remained long unknown or misunderstood for this reason. The earlier anatomists supposed that the arteries were tubes for the circulation of air, because they appeared empty when opened after death. It was only when Galen exposed the artery of a living animal, and, opening it between two ligatures, showed it to be full of blood, that the true function of these vessels was ascertained. The lacteal and lymphatic vessels were discovered in the seventeenth century; but from their small size, and the small amount of fluid contained in them, the circulation in the lymphatic system was thought to be very limited in quantity. Two hundred years afterward, when the experiment was performed of introducing a canula into the thoracic duct of the living animal and continuing the observation while digestion and absorption were going on, the experimenters obtained, in horses and oxen, from fifty to one hundred pounds of lymph and chyle during twenty-four hours; thus demonstrating the existence of a vital activity much greater than could have been suspected from any examination of the dead body.

The observation of the physiological actions during life usually requires the employment of certain contrivances and manipulations in order to arrive at accurate results. Even the more superficial phenomena, such as the changes in the air produced by respiration, can only be studied with precision by the aid of artificial means for measuring and examining the various gases absorbed or discharged. The processes going on in the internal organs are more especially concealed from view, and, therefore, need for their study the use of instruments and operations in order to bring them under observation. It is accordingly necessary, in the large majority of cases, to resort to experiments upon animals in the study of physiology, and all the important knowledge thus far gained has been acquired in this way. But as the physiology of the human species is the main object of our study, and as each different species of animals presents certain peculiarities which distinguish it from others, it becomes essential to know how far we can apply the results derived from experiment upon one species to the physiology of the others, or to that of the human body itself.

All animals present certain general phenomena in common, namely, those of nutrition, secretion, absorption, movement, and reproduction. The vertebrate animals, to which class man belongs, are furthermore constructed upon the same general plan of organization, and their corresponding organs are evidently the same in character. The different parts of their nervous and vascular systems, their digestive apparatus, their organs of locomotion, of secretion, excretion, and reproduction, have the same relative position, and can be easily recognized and compared with each other. The ingredients of their solids and fluids have the same or a similar chemical constitution, and play a corresponding part in the vital processes. The coloring matter of the blood is identical in all of them; they all absorb oxygen and exhale carbonic acid with more or less activity; and many or most of their

secretions and excretions have the same physiological character. The whole value of physiological experiment, as applied to different species, depends upon this general resemblance between them, both of structure and function.

On the other hand, the differences between species of vertebrate animals consist only in the relative size and development of particular parts, and consequently in the relative importance of particular functions. The intestine, for example, is longer and more complicated in the herbivorous animals, shorter and simpler in the carnivora. The muscles of the external ear are slightly developed and powerless in the human subject, large and active in many of the inferior species. Fish and reptiles produce but little animal heat, and are, therefore, called *cold-blooded* animals; birds and quadrupeds generate it in abundance, and are therefore called *warm-blooded*. The differences between them are, therefore, almost invariably differences in degree and not in kind.

Consequently the simple and direct result of an experiment in different animals is the same, or varies only in degree. If we deprive an animal of oxygen, whatever the species may be, it produces death invariably and in the same way, because in all this element is essential to the nourishment of the tissues. But death will take place rapidly in birds or quadrupeds, more slowly in reptiles, because the vital changes are more active in the former than in the latter. Division of the spinal cord in all cases produces immediate paralysis of sensation and voluntary motion in the parts below, showing that the sensitive and motor fibres follow in all the same route and possess the same nervous endowments. Experiments accordingly of the same kind, performed upon different animals, have a direct result which is the same in character.

But experiments have often also certain *indirect* or secondary results, dependent upon the relative importance of associated organs, and these vary considerably in different kinds of animals. Thus division or disease of the facial nerve in all instances causes a direct paralysis of the muscles of the face. In the human subject this produces only a loss of expression, with some inconvenience in the retention of fluids by the mouth. But in the horse it is followed by a partial suffocation, because in him the expansion of the nostrils is an important part of the movements of respiration. While the direct effect of an experiment, therefore, is always the same, its indirect effect varies with the comparative development of different parts. It is evident, however, that this variation does not impair the value of experiment as a means of study, but, on the contrary, enlarges its usefulness and leads to the acquisition of greater knowledge by its means.

The physiological actions of living beings are, of course, dependent upon natural causes, and are to be studied in a similar manner with other natural phenomena, such as those of magnetism, gravitation, chemical affinity, and the like. In all these cases, we observe the character of the phenomenon, the conditions upon which it depends, the mechanism of its production, and the quantities of force or material

expended in its manifestation. The study of physiology, therefore, requires a certain knowledge of the chemical and physical reactions presented in the outer world, in order that the observer may be able to appreciate the peculiarities of similar phenomena as they occur in the living body. As all animated beings are closely dependent on external conditions for the maintenance of their vitality, it is evident that the study of their vital actions cannot be disconnected from that of external natural phenomena. The pressure and tension of the atmosphere, for example, as well as its chemical constitution, are directly connected with the process of respiration; and the circulation of the blood through the vessels exhibits the physical phenomena of an incompressible fluid flowing through elastic tubes.

By the term *vital phenomena*, accordingly, we mean those phenomena which are manifested in the living body, and which are characteristic of its functions. At the same time many of them do not differ in character from those of the outside world, but only in the peculiarity of their conditions and their results.

Some of these phenomena are physical or mechanical in their character; as, for example, the play of the articulating surfaces upon each other, the balancing of the spinal column with its appendages, the action of the elastic ligaments. Nevertheless, these phenomena, though strictly physical in character, are often entirely peculiar and different from those seen elsewhere, because the mechanism of their production is peculiar in its details. Thus the human voice and its modulations are produced in the larynx, in accordance with the general physical laws of sound; but the arrangement of the elastic and movable vocal chords, and their relations with the columns of air above and below, the moist and flexible mucous membrane, and the contractile muscles outside, are of such a special character that the entire apparatus, as well as the sounds produced by it, is peculiar; and its action cannot be properly compared with that of any other known musical instrument.

In the same manner, the movements of the heart are so complicated and remarkable that they cannot be comprehended, even by one who is acquainted with the anatomy of the organ, without a direct examination. This is not because there is anything essentially obscure or mysterious in their nature, for they are purely mechanical in character; but because their conditions are so peculiar, owing to the tortuous course of the muscular fibres, their arrangement in interlacing layers, their attachments and relations, that their combined action produces an effect altogether peculiar, and one which is not similar to anything outside the living body.

A very large and important class of the vital phenomena are those of a chemical character. It is one of the characteristics of living bodies that a succession of chemical actions, combinations, and decompositions, is constantly going on in their interior. It is one of the necessary conditions of the existence of every animal and every vegetable, that it should constantly absorb various substances from without, which under-

go different chemical alterations in its interior, and are finally discharged from it under other forms. If these changes be prevented from taking place, life is immediately extinguished. Thus animals constantly absorb, on the one hand, water, oxygen, salts, albumen, oil, sugar, etc., and give up, on the other hand, to the surrounding media, carbonic acid, water, creatine, the urates, urea, and the like; while between these two extreme points, of absorption and exhalation, there take place a multitude of different transformations which are essential to the continuance of life.

Some of these chemical actions are the same with those which are seen outside the body; but most of them are peculiar, and do not take place anywhere else. This, again, is not because there is anything exceptional in their *nature*, but because the conditions necessary for their accomplishment exist in the body, and do not exist elsewhere. All chemical phenomena are liable to be modified by surrounding conditions. Many reactions which will take place at a high temperature will not take place at a low temperature, and *vice versâ*. Some will take place in the light, but not in the dark; others will take place in the dark, but not in the light. Because a chemical reaction, therefore, takes place under one set of conditions, we cannot be at all sure that it will take place under others which are different.

The chemical conditions of the living body are exceedingly complicated. In the animal solids and fluids, there are many substances mingled together in varying quantities, which modify or interfere with each other's reactions. New substances are constantly entering by absorption, and old ones leaving by exhalation; while the circulating fluids are incessantly passing from one part of the body to another, and coming in contact with different organs of different texture and composition. All these conditions are peculiar, and so modify the chemical actions taking place in the body that they are often unlike those met with elsewhere.

If starch and iodine be mingled together in a watery solution, they unite with each other, and strike a deep blue color; but if they be mingled in the blood, no such reaction takes place, because it is prevented by the presence of certain organic substances which interfere with it.

If dead animal matter be exposed to warmth, air, and moisture, it putrefies; but if introduced into the living stomach, this process is prevented, because the fluids of the stomach cause the animal substance to undergo a peculiar transformation (digestion), after which the blood-vessels immediately remove it by absorption. There are also certain substances which make their appearance in the living body of animals or vegetables, and which are not found elsewhere; such as fibrine, albumen, caseine, the biliary salts, hemoglobine, chlorophyll, morphine, etc. These substances cannot be manufactured artificially, simply because we are unable to imitate the necessary conditions. They require for their production the presence of a living organism.

The chemical phenomena of the living body are, therefore, not different

in their nature from any other chemical phenomena; but they are often different in their conditions and in their results, and are consequently peculiar and characteristic.

Another set of vital phenomena are those which are manifested in the processes of reproduction and development. They are entirely distinct from any phenomena which are exhibited by matter not endowed with life. An inorganic substance, even when it has a definite form, as, for example, a crystal of fluor spar, has no particular relation to any similar form which has preceded, or any other which is to follow it. On the other hand, every animal and every vegetable owes its origin to preceding animals or vegetables of the same kind; and the manner in which this production takes place, and the different forms through which the new body successively passes in the course of its development, constitute the phenomena of reproduction. These phenomena are mostly dependent on the chemical processes of nutrition and growth, which take place in a particular direction and in a particular manner; but their results, namely, the production of a connected series of different forms, constitute a separate class of phenomena, which cannot be explained in any manner by the preceding, and require, therefore, to be studied by themselves.

Another set of vital phenomena are those which belong to the nervous system. These, like the processes of reproduction and development, depend on the chemical changes of nutrition and growth. That is to say, if the nutritive processes did not go on in a healthy manner and maintain the nervous system in a healthy condition, the peculiar phenomena which are characteristic of it could not take place. The nutritive processes are necessary conditions of the nervous phenomena. But there is no other connection between them; and the nervous phenomena themselves are distinct from all others, both in their nature and in the mode in which they are to be studied.

The study of Physiology is naturally divided into three distinct Sections:—

I. The first of these includes everything which relates to the Nutrition of the body in its widest sense. It comprises the history of the proximate principles, their source, the manner of their production, the proportions in which they exist in different kinds of food and drink, the processes of digestion and absorption, and the constitution of the circulating fluids; then, the physical phenomena of the circulation and the forces by which it is accomplished; the changes which the blood undergoes in different parts of the body; all the phenomena, both physical and chemical, of respiration; those of secretion and excretion, and the character and destination of the secreted and excreted fluids. All these processes have reference to a common object, namely, the preservation of the normal structure and organization of the individual. Their results comprise the phenomena of internal growth and nutrition, which are common to the animal and vegetable kingdoms; and they are accordingly known by the name of the *vegetative functions.*

II. The second Section, in the natural order of study, is devoted to the phenomena of the Nervous System. These phenomena are not exhibited by vegetables, but belong exclusively to animal organizations. They bring the animal body into relation with the external world, and preserve it from external dangers, by means of sensation, movement, consciousness, and volition. They are more particularly distinguished by the name of the *animal functions.*

III. Lastly comes the study of the entire process of Reproduction. Its phenomena, again, with certain modifications, are met with in both animals and vegetables; and might, therefore, with some propriety, be included under the head of vegetative functions. But their distinguishing peculiarity is, that they have for their object the production of new organisms, which take the place of the old and remain after they have disappeared. These phenomena do not, therefore, relate to the preservation of the individual, but to that of the species; and any study which concerns the species comes properly after we have finished everything relating to the individual.

SECTION I.

NUTRITION.

CHAPTER I.

PROXIMATE PRINCIPLES IN GENERAL.

THE study of NUTRITION begins naturally with that of the *proximate principles*, or the substances entering into the composition of the different parts of the body, and the different kinds of food. In examining the body, the anatomist finds that it is composed, first, of various parts, which are easily recognized by the eye, and which occupy distinct situations. In the case of the human body, for example, a division is easily made of the entire frame into the head, neck, trunk, and extremities. Each of these regions, again, is found, on examination, to contain several distinct parts, or "organs," which require to be separated from each other by dissection, and which are distinguished by their form, color, texture, and consistency. In a single limb, for example, every bone and every muscle constitutes a distinct organ. In the trunk, we have the heart, the lungs, the liver, spleen, kidneys, spinal cord, etc., each of which is also a distinct organ. When a number of organs, differing in size and form, but similar in texture, are found scattered throughout the entire frame, or a large portion of it, they form a connected set or order of parts, which is called a "system." Thus, all the muscles taken together constitute the muscular system; all the bones, the osseous system; all the arteries, the arterial system. Several entirely different organs may also be connected with each other, so that their associated actions tend to accomplish a single object, and they then form an "apparatus." Thus the heart, arteries, capillaries, and veins, together, form the circulatory apparatus; the stomach, liver, pancreas, intestines, etc., the digestive apparatus. Every organ, again, on microscopic examination, is seen to be made up of minute bodies, of definite size and figure, which are so small as to be invisible to the naked eye, and which, after separation from each other, cannot be further subdivided without destroying their organization. They are, therefore, called "anatomical elements." Thus, in the liver, there are hepatic cells, capillary blood-vessels, the fibres of Glisson's capsule, and the ultimate filaments of the

hepatic nerves. Lastly, two or more kinds of anatomical elements interwoven with each other in a particular manner form a "tissue." Adipose vesicles, with capillaries and nerve filaments, form adipose tissue. White fibres, elastic fibres, and connective-tissue cells, with capillary bloodvessels and nerve filaments, form connective tissue. Thus the solid parts of the entire body are made up of anatomical elements, tissues, organs, systems, and apparatuses. Every organized frame, and even every apparatus, every organ, and every tissue, is made up of different parts, variously interwoven and connected with each other, and it is this character which constitutes its *organization.*

But beside the above solid forms, there are also certain fluids, which are constantly present in various parts of the body, and which, from their peculiar constitution, are termed "animal fluids." These fluids are just as much an essential part of the body as the solids. The blood and the lymph, for example, the pericardial and synovial fluids, the saliva, which always exists more or less abundantly in the ducts of the parotid gland, the bile in the biliary ducts and the gall-bladder: all these go to make up the entire body, and are quite as necessary to its physiological structure as the muscles or the nerves. Now, if these fluids be examined, they are found to be made up of many different substances, which are mingled together in certain proportions; these proportions being constantly maintained at or about the same standard by the natural processes of nutrition. Such a fluid is termed an *organized fluid.* It is organized by virtue of the numerous ingredients which enter into its composition, and the regular proportions in which these ingredients are maintained. Thus in the plasma of the blood, we have albumen, fibrine, water, chlorides, carbonates, and phosphates. In the urine, we find water, urea, sodium urate, creatinine, coloring matter, and salts. These substances, which are mingled together so as to make up, in each instance, by their intimate union, a homogeneous liquid, are called the PROXIMATE PRINCIPLES of the animal fluid.

In the solids, furthermore, even in those parts which are apparently homogeneous, there is a similar mixture of various ingredients. In the hard substance of bone, for example, there is, first water, which may be expelled by evaporation; second, lime phosphate and carbonate, which may be extracted by the proper solvents; third, a peculiar animal matter, with which these calcareous salts are in union; and fourth, various other saline substances, in special proportions. The muscular tissue contains water, sodium and potassium chlorides, lime phosphate, creatine, various forms of albumen, and an animal matter termed myosine. The difference in consistency between the solids and fluids does not, therefore, indicate any radical difference in their constitution. Both are equally made up of proximate principles, mingled together in various proportions.

It is important to understand, however, exactly what are proximate principles, and what are not such; for since these principles are extracted from the animal solids and fluids, and separated from each

other by the help of certain chemical manipulations, such as evaporation, solution, crystallization, and the like, it might be supposed that every substance which could be extracted from an organized solid or fluid, by chemical means, should be considered as a proximate principle. That, however, is not the case. A proximate principle is properly defined to be *any substance, whether simple or compound, chemically speaking, which exists, under its own form, in the animal solid or fluid*, and which can be extracted by means which do not alter or destroy its chemical properties. Lime phosphate, for example, is a proximate principle of bone, but phosphoric acid is not so, since it does not exist as such in the bony tissue, but is produced only by the decomposition of the calcareous matter ; still less phosphorus, which is obtained only by the decomposition of the phosphoric acid.

Proximate principles may, in fact, be said to exist in all solids or fluids of mixed composition, and may be extracted from them by the same means as in the case of the animal tissues or secretions. Thus, in a watery solution of sugar, we have two proximate principles, namely: first, the water, and secondly, the sugar. The water may be separated by evaporation and condensation, after which the sugar remains behind, in a crystalline form. These two substances have, therefore, been simply separated from each other by the process of evaporation. They have not been decomposed, nor their chemical properties altered. On the other hand, the hydrogen and oxygen of the water were not proximate principles of the original solution, and did not exist in it under their own forms, but only in a state of combination; forming, in this condition, a fluid substance (water), endowed with sensible properties entirely different from theirs. If we wish to ascertain, accordingly, the nature and properties of a saccharine solution, it will afford us but little satisfaction to extract its ultimate chemical elements; for its nature and properties depend not so much on the presence in it of the ultimate elements, oxygen, hydrogen, and carbon, as on the particular forms of combination, namely, water and sugar, under which they are present.

It is very essential, therefore, that in extracting the proximate principles from the animal body, only such means should be adopted as will isolate the substances already existing in the tissues and fluids, without decomposing them, or altering their nature. A neglect of this rule would lead to erroneous results in the pursuit of physiological chemistry; for by subjecting the animal tissues to the action of acids and alkalies, of prolonged boiling, or of too intense heat, we might obtain, at the end of the analysis, substances which would not be, properly speaking, proximate principles, but only the remains of an altered and disorganized material. Thus, the fibrous tissues, if boiled steadily for thirty-six hours, dissolve, for the most part, at the end of that time, in the boiling water; and on cooling the whole solution solidifies into a homogeneous, jelly-like substance, which has received the name of *gelatine*. But this gelatine does not really exist in the body as a

proximate principle, since the fibrous tissue which produces it is not at first soluble, even in boiling water, and its ingredients become altered and converted into a gelatinous matter only by prolonged ebullition. So, again, an animal substance containing the alkaline acetates or lactates will, upon incineration in the air, yield carbonates of the same bases, the original acid having been destroyed, and replaced by carbonic acid. In either case, the analysis of the tissue, so conducted, would be a deceptive one, and useless for anatomical and physiological purposes, because its real ingredients have been decomposed, and replaced by others, in the process of manipulation.

It should, therefore, be kept constantly in view, in the examination of an animal tissue or fluid, that the object of the operation is simply *the separation of its ingredients from each other*, and not their decomposition or ultimate analysis. Only the simplest forms of chemical manipulation, if possible, should be employed. The substance to be examined should first be subjected to evaporation, in order to extract and estimate its water. This evaporation must be conducted at a heat not above 100° (212° F.), since a higher temperature would destroy or alter some of the animal ingredients. Then, from the dried residue, sodium chloride, alkaline sulphates, carbonates, and phosphates may be extracted with water. Coloring matters may be separated by alcohol, and oils may be dissolved out by ether. When a chemical decomposition is unavoidable, it must be kept in sight and afterward corrected. Thus the sodium glyko-cholate of the bile is separated from certain other ingredients by precipitating it with plumbic acetate, forming lead glyko-cholate; but this is afterwards decomposed, in its turn, by sodium carbonate, reproducing the original sodium glyko-cholate. Sometimes it is impossible to extract a proximate principle in an entirely unaltered form. Thus the fibrine of the blood can be separated only by allowing it to coagulate; and once coagulated, it is permanently altered, and no longer presents its original characters as an ingredient of the blood. In such instances as this, we can only make allowance for an unavoidable difficulty, and endeavor by other means to ascertain under what form the substance originally existed in the animal fluids, being careful that the substance suffers no further alteration. By bearing in mind the above considerations, we may form a tolerably correct estimate of the nature and quantity of all the proximate principles in the tissue or fluid under examination.

The manner in which the proximate principles are associated together is also deserving of notice. In every animal solid and fluid, there is a considerable number of proximate principles which are present in certain proportions, and which are so united with each other that the mixture presents a homogeneous appearance. But this union is of a complicated character; and the presence of each ingredient depends, to a certain extent, upon that of the others. Some of them, such as the alkaline carbonates and phosphates, are in solution directly in the water. Some, which are insoluble in water, are retained in solu-

tion by the presence of other soluble substances. Thus, the insoluble lime phosphate of the urine is held in solution by the acid reaction of the sodium biphosphate, which is also present as an ingredient. In the alkaline blood-plasma, on the other hand, the lime phosphate is liquefied by union with the albumen, which is itself soluble in the water of the plasma. The same substance may be fluid in one part of the body, and solid in another part. Thus in the blood and secretions the water is fluid, and holds in solution other substances, both animal and mineral, while in the bones and cartilages it is solid—not crystallized, as in ice, but amorphous and solid, by the fact of its intimate union with the animal and saline ingredients, which are abundant in quantity, and which are themselves present in the solid form. Again, the lime phosphate of the blood is fluid by solution in the albumen; but in the bones it forms a solid substance with the animal matter of the osseous tissue; and yet the union of the two is as intimate and homogeneous in the bones as in the blood. A proximate principle, therefore, never exists alone in any part of the body, but is always intimately associated with a number of others, by a kind of homogeneous mixture or mutual solution.

Every animal tissue and fluid contains a number of proximate principles which are present, as we have already mentioned, in certain characteristic proportions. Thus, water is present in very large quantity in the perspiration and the saliva, but in very small quantity in the bones and teeth. Sodium chloride is comparatively abundant in the blood and deficient in the muscles. On the other hand, potassium chloride is more abundant in the muscles, less so in the blood. But these proportions are nowhere absolute or invariable. There is a great difference, in this respect, between the chemical composition of an inorganic substance and the physiological constitution of an animal fluid. The former is always constant and definite; the latter always presents certain variations. Thus, water is always composed of exactly the same relative quantities of hydrogen and oxygen; and if these proportions be altered in the least, it thereby ceases to be water, and is converted into some other substance. But in the urine, the proportions of water, urea, urates, phosphates, etc., vary within certain limits in different individuals, and even in the same individual, from one hour to another. This variation, which is almost constantly taking place, within the limits of health, is presented by all the animal solids and fluids. It is even a necessary accompaniment of the actions of life, and one of the characteristic phenomena of living beings. For all parts of the body are composed of different ingredients which are supplied by absorption or formed in the interior, and which are constantly given up again, under the same or different forms, to the surrounding media by the unceasing activity of the vital processes. Every variation, then, in the general condition of the body, as a whole, is accompanied by a corresponding variation, more or less pronounced, in the constitution of its different parts. This constitution is consequently of a very dif-

ferent character from the chemical constitution of an oxide or a salt. Whenever, therefore, we meet with the analysis of an animal fluid, in which the relative quantity of its different ingredients is expressed in numbers, we must understand that such an analysis is always approximative, and not absolute.

The proximate principles are naturally divided into five different classes.

The first of these classes comprises all the proximate principles which are purely INORGANIC in their nature. These principles are derived mostly from the exterior. They are found everywhere, in the inorganic world as well as in organized bodies; and they present themselves under the same forms and with the same properties in the interior of the animal frame as elsewhere. They are crystallizable, and they present very definite chemical characters and have a comparatively simple chemical constitution. They are compounds, in simple proportions, of the ultimate chemical elements, hydrogen and oxygen, the metals of the alkaline and earthy salts, sulphur, phosphorus, chlorine, and, in general terms, of the ingredients of mineral substances. They comprise water, which is the most abundant of its class in the animal frame, sodium and potassium chlorides, phosphates, and sulphates, alkaline carbonates, the salts of lime and magnesia, together with combinations of a few other of the metallic elements in minute quantity.

The second class of proximate principles consists of the HYDROCARBONACEOUS SUBSTANCES of organic origin. They are distinguished from inorganic matters first by the fact of their containing *carbon* in large proportion as one of their immediate constituents, associated always with hydrogen and oxygen, but with no other chemical element. They are always either crystallizable, or else readily convertible into other crystallizable members of the same group. Their chemical composition is less simple than that of inorganic substances, but it is still sufficiently definite, and their chemical characters are well marked and easily recognizable. They first make their appearance in the interior of organized bodies, and are not found in the inorganic world, excepting as the remains or products of animal or vegetable life. To this group belong the several varieties of starch, sugar, and oil.

The third class comprises the ALBUMINOUS, or nitrogenized proximate principles. These substances derive their name from the albumen or white of egg, which was one of the earliest to be studied, and which was long considered as a kind of representative of the whole class. They differ from the substances of the two preceding groups, especially in the fact that they contain *nitrogen* as an ingredient, in addition to the three elements of the hydrocarbonaceous matters. They are exclusively of organic origin, appearing only as ingredients of the living body. Their chemical constitution, furthermore, is a complicated one—that is, their four elements are united with each other in such a way as to form compounds of a very high atomic weight. Their chemical characters

are not well defined, as compared with those of inorganic substances, and their most striking properties are not such as can be accounted for by ordinary chemical reactions or expressed in the usual chemical phraseology. Nevertheless, they are of the first importance as ingredients of the organized frame, since they form a large proportion of its mass, and contribute, by their peculiar properties, to its most essential and characteristic active phenomena. They include such substances as albumen, fibrine, caseine, and myosine.

The fourth class is formed by the COLORING MATTERS. These substances, upon which the different tints of the solids and fluids depend, are present, for the most part, in small quantity, the most abundant being the red coloring matter of the blood.

Lastly, in the fifth class are comprised a group of CRYSTALLIZABLE NITROGENOUS MATTERS, many, if not all, of which are derived from the physiological metamorphosis of albuminous principles. They are found in some of the solid tissues, as the brain and nerves, in the secretions of the liver, and especially in the urine, where they represent the products of excretion.

CHAPTER II.

INORGANIC PROXIMATE PRINCIPLES.

THE *inorganic* substances are present in the animal body in great variety. Some of them, such as water and the salts of lime, constitute also a large proportion of the mass of the tissues and fluids in which they are found; others present themselves in comparatively small quantity. Some of them are found universally in all regions of the body, while others are met with only in particular tissues or fluids; but there are hardly any which do not appear at the same time as constituents of several different parts. As their name indicates, these substances are met with extensively in the inorganic world, and form a large part of the crust of the earth. Notwithstanding, however, their inorganic nature, they are also essential constituents of the animal frame. They are accordingly necessary ingredients of the food and drink, and no regimen would be capable of supporting life indefinitely which did not contain these materials in due proportion.

The group of inorganic proximate principles includes the following substances:—

Water;	Potassium phosphate;
Sodium chloride;	Potassium sulphate;
Sodium phosphate;	Potassium carbonate;
Sodium biphosphate;	Lime phosphate;
Sodium sulphate;	Lime carbonate;
Sodium carbonate;	Magnesium phosphate;
Potassium chloride;	Magnesium carbonate.

Beside the above-named proximate principles there are found, as constant ingredients of the incombustible residue of various parts of the human body, iron, silica, and fluorine; but it is not certainly known in what form of combination these substances originally existed in the animal solids and fluids. Sometimes, but not always, there are indications of the presence, in minute quantity, of copper, manganese, and lead, also in some unknown forms of combination.

The most important of the inorganic proximate principles, considered in regard to their quantity or the part which they play in the vital actions, are the following:—

1. **Water,** H_2O.

Water is universally present in all the tissues and fluids of the body. It is abundant in the blood and secretions, where its presence is indis-

pensable in order to give them the fluidity which is necessary to the performance of their functions; for it is by the blood and secretions that new substances are introduced into the body, and old ingredients discharged. And it is a necessary condition both of the introduction and discharge of substances naturally solid, that they assume, for the time being, a fluid form; water is therefore an essential ingredient of the fluids, for it holds their solid materials in solution, and enables them to pass and repass through the animal frame.

But water is an ingredient also of the solids. For if we take a muscle or a cartilage, and expose it to a gentle heat in dry air, it loses water by evaporation, diminishes in size and weight, and becomes dense and stiff. Even the bones and teeth lose water by evaporation in this way, though in smaller quantity. In all these solid and semi-solid tissues, the water which they contain is useful by giving them the special consistency which is characteristic of them, and which would be lost without it. Thus a tendon, in its natural condition, is white, glistening, and opaque; and though very strong, perfectly flexible. If its water be expelled by evaporation it becomes yellowish in color, shrivelled, semi-transparent, inflexible, and unfit for performing its mechanical functions. The same thing is true of the other tissues, such as that of the skin, the muscles, the cartilages, and the glands.

The following is a list, compiled by Robin and Verdeil from various observers, showing the proportion of water per thousand parts, in different solids and fluids:—

Quantity of Water in 1000 parts in

Teeth	100	Bile	880
Bones	130	Milk	887
Cartilage	550	Pancreatic juice	900
Muscles	750	Urine	936
Ligaments	768	Lymph	960
Brain	789	Gastric juice	975
Blood	795	Perspiration	986
Synovial fluid	805	Saliva	995

According to the best calculations, water constitutes, in the human subject, about seventy per cent. of the entire weight of the body.

The water which thus forms a part of the animal frame is derived mainly from without. It is taken in the different kinds of drink, and also forms an abundant ingredient in the various articles of food. For no articles of food are taken in an absolutely dry state, but all contain a larger or smaller quantity of water, which may readily be expelled by evaporation. The quantity of water, therefore, which is daily taken into the system, cannot be ascertained in any case by simply measuring the quantity of drink, but its proportion in the solid food, taken at the same time, must also be determined by experiment, and this ascertained quantity added to that which is taken in with the fluids. By measuring the quantity of fluid taken with the drink, and calculating in addition

4

the proportion existing in the solid food, we have found, in common with the results formerly obtained by Barral, that, for a healthy adult man, the average quantity of water introduced into the system is about 2000 grammes per day.

There is every reason to believe that a certain quantity of water also makes its appearance within the body by the liberation of its elements from various organic combinations. This is shown by the fact that a considerable quantity of hydrogen is daily introduced into the system as a constituent element of the organic substances of the food, while only a small part of this quantity reappears, under similar forms of combination, in the excretions. The most reliable estimates, in this respect, are as follows:—

Average Daily Quantity of Hydrogen

Introduced in organic combinations with the food	40 grammes.
Discharged " " " excretions . . .	6 "
Residue unaccounted for	34 "

Thus not more than fifteen per cent. of the quantity introduced is discharged in the organic ingredients of the excretions. But no hydrogen is exhaled from the body in a free state, nor in notable quantity in any other form of inorganic combination except water. The surplus must, therefore, pass out as part of the water or watery vapor which is constantly being discharged from various organs. The estimates given above indicate that a little over 300 grammes of water are daily produced in the body in this way. As we shall hereafter see, an important class of the organic ingredients of the food already contain hydrogen and oxygen in the relative quantities necessary to form water; and, when decomposed in the system, may readily yield these elements in the required proportions.

Furthermore, although it has not yet been proved, in any particular case, that more water is discharged from the system than can be accounted for by that introduced, yet a comparison of the average results obtained by different observers, always tends to show a surplus of water in the entire excretions, varying from 200 to 500 grammes over and above that introduced with the food and drink. The quantity of water, however, thus produced in the body is small in comparison with that which is introduced and discharged under its own form.

While in the interior of the living body, water takes part in the vital functions principally by its physical properties. It is the universal solvent for all the ingredients of the animal fluids, holding them in solution either by its direct liquefying power, or by the aid of other substances which are themselves soluble. It thus enables the nutritious elements of the food to find their way into the circulating fluid, and to penetrate the substance of the solid organs. It permeates the organized membranes of the body and brings into contact with each other the inorganic and organic materials of various parts, and enables them to

assume new forms by their mutual reactions. In this way it is subservient to all the phenomena of absorption, transudation, exhalation, and even of chemical union and decomposition, which make up the internal nutritive functions of the animal frame.

After forming part of the animal solids and fluids, and playing its part in the vital processes of the interior, the water is again discharged; for its presence in the body, like that of all the other proximate principles, is not permanent, but only temporary. It makes its exit from the body by four different passages: namely, in a liquid form with the urine and feces, and in the form of vapor by the lungs and skin. The actual quantity which is expelled in each case is not uniform, but varies according to circumstances. Thus, if the kidneys be unusually active, the watery ingredients of the urine will be temporarily increased in quantity, while the cutaneous perspiration will be diminished; and the state of the atmosphere and the rapidity of respiration will influence for the time the amount of watery vapor exhaled by the lungs and skin. Still there is a well-marked average relation between the functional activity of the various organs and the daily quantity of their excreted fluids. It appears from a comparison of the researches of Lavoisier and Seguin, Valentin, and other observers, that the water which is thus discharged from the system finds its way out by these different routes nearly in the following proportions:—

By exhalation from the lungs	20 per cent.
By the cutaneous perspiration	30 "
By the urine and feces	50 "

While only four per cent. of the water is expelled with the feces, ninety-six per cent. passes out by the lungs, the skin, and the kidneys. It is evident, therefore, that at least the main bulk of the water taken in with the food does not simply pass through the alimentary canal, but is taken up by the mucous membranes, enters the circulating fluid, and forms a temporary constituent of the solid tissues of the body. As it appears in the secretions it also brings with it various ingredients which it has absorbed from the substance of the glandular organs; and when finally discharged it is mingled in the urine and feces with salts and excrementitious matters, which it holds in solution, and in the cutaneous and pulmonary exhalations, with animal vapors and odoriferous materials of various kinds. In the perspiration it also contains mineral sulphates and chlorides, which it leaves behind on evaporation.

2. Lime Phosphate, $Ca_3P_4O_8$.

This substance exists as an ingredient of all the animal solids and fluids without exception. So far as regards its mass, it is, next to water, the most important of the inorganic constituents of the body, as its entire quantity is far greater than that of any other of the mineral salts. For, although it is not especially abundant in the fluids and

the softer tissues, it forms more than one-half the substance of the bones. It is estimated by Barral, that the osseous tissues constitute 6.4 per cent. of the entire mass of the body; and the lime phosphate forms on the average from 57 to 58 per cent. of the substance of the bones. This would give, for a man weighing 65 kilogrammes, or 143 pounds avoirdupois, 2400 grammes of the calcareous salt in the whole body. Its proportion in various tissues and fluids of the human system is as follows:—

Quantity of Lime Phosphate in 1000 Parts in the

Enamel of the teeth	885	Milk	2.72
Dentine	643	Blood	0.30
Bones	576	Bile	0.92
Cartilages	40	Urine	0.75

Notwithstanding, therefore, the large quantity of lime phosphate in the body as a whole, it is evident, from an inspection of the preceding list, that nearly all of it is deposited in the more solid tissues; while it is present in but slender proportion in the animal fluids. Of these fluids it is the milk alone which contains lime phosphate in notable quantity, and here it is plainly subservient to the ossification of the growing bones of the young infant, for whom the milk is used as food. In the circulating fluids, the internal secretions, and the urine, on the other hand, the calcareous salt is in small amount. Its importance in the body depends mainly upon its simple physical property of imparting rigidity to the solid tissues, rather than upon its active qualities in the general phenomena of nutrition.

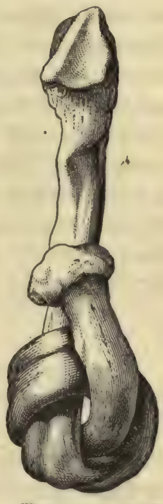
In the solid tissues it is associated with other earthy and alkaline salts, but preponderates largely over them in amount. In the bones, the quantity of lime phosphate is from 5 to 6 times greater than that of all the other mineral ingredients taken together.

In the bones, teeth, and cartilages, the lime phosphate exists in a solid form; not, however, deposited mechanically in the osseous or cartilaginous substance as a granular powder, but intimately united with the animal matter of the tissues, like coloring matter in colored glass, the union of the two forming a homogeneous material. It is not, on the other hand, so combined with the animal matter as to lose its identity and constitute a new chemical substance, as where hydrogen combines with oxygen to form water; but rather as salt unites with water in a saline solution, both substances retaining their original character and composition, though so intimately associated that they cannot be separated by mechanical means. The lime phosphate, therefore, may be extracted from a bone by maceration in dilute muriatic acid, leaving behind the animal substance, which still retains the original form of the bone or cartilage.

In all the solid tissues the lime phosphate is useful by giving to them their proper consistence and solidity. For example, in the enamel of the teeth, the hardest tissue of the body, it predominates very

much over the animal matter, and is present in greater abundance there than in any other part of the frame. In the dentine, a softer tissue, it is in somewhat smaller quantity, and in the bones smaller still; though in the bones it continues to form more than one-half the entire mass of the osseous tissue. The importance of this substance, in communicating to bones their natural stiffness and consistency, may be readily shown by the alteration which they suffer from its removal. If a long bone be macerated in dilute muriatic acid, the earthy salt, as already mentioned, is dissolved out, after which the bone loses its rigidity, and may be bent or twisted in any direction without breaking. (Fig. 1.)

Fig. 1.



FIBULA TIED IN A KNOT, after maceration in a dilute acid. (From a specimen in the museum of the College of Physicians and Surgeons.)

In the formation of the bony skeleton, during fœtal life, infancy, and childhood, the cartilaginous substance previously existing is replaced by osseous matter, which contains a larger proportion of calcareous salts; while the anatomical texture of the parts is also changed, giving rise to the characteristic forms of bony tissue. This progressive consolidation of the framework of the body is known as the process of "ossification." In some instances this process is defective, owing to partial failure in the powers of assimilation; and as the rigidity of the skeleton, accordingly, does not increase as it should do in proportion to the weight of the body and to muscular action, the bones become gradually bent and deformed, sometimes to an extraordinary degree. This affection has received the name of *Rachitis*.

A somewhat similar result is produced by a morbid softening of the bones, which sometimes comes on in adult life, known as *Osteomalakia*. In this disease the bony fabric, after its formation, becomes altered in texture and composition; and, the new substance which takes its place being deficient in calcareous matter, a progressive yielding and deformity of the skeleton takes place, like that which happens in cases of rachitis.

In the plasma of the blood the lime phosphate, though insoluble in simple alkaline watery liquids, is held in solution by its union with the albuminous ingredients. It has been shown by Fokker that the earthy phosphates added to white of egg unite with the albuminous matter and become soluble in considerable proportion. This explains the presence of lime phosphate in a liquid form both in the blood and in the milk, both fluids which have an alkaline reaction. In the urine, on the other hand, it is held in solution by the presence of the acid sodium biphosphate. Accordingly, whenever the urine is rendered alkaline by the addition of soda or potassa, the earthy phosphates are precipitated in the form of a white turbidity.

The source of the lime phosphate of the animal solids and fluids is in the food. This substance exists in nearly every animal and vegetable alimentary matter in common use. It is found not only in muscular flesh, eggs, and milk, and in all the cereal grains, as wheat, rye, oats, barley, maize, and rice, but also in peas and beans, the nutritive tubers and roots, as potatoes, beets, turnips, and carrots, and even in the juicy fruits, such as the apple, pear, plum, and cherry.

After forming for a time a constituent part of the body, the lime phosphate is again discharged with the excretions, but very slowly and in small amount. According to the observations of Neubauer and Beneke about 0.4 gramme, on the average, is daily expelled with the urine. A slightly larger quantity is also found in the feces, but this may be only the residue derived from the undigested portion of the food. Only traces of it are to be detected in the perspiration. As so large a quantity of this salt, therefore, is contained in the body, while so small a proportion is expelled daily with the excretions, it is evidently to be regarded as one of the more permanent constituents of the frame; being comparatively inactive in the process of internal metamorphosis, and serving for the most part as a physical ingredient of the solid tissues.

3. Lime Carbonate, $CaCO_3$.

Lime carbonate is to be found in the bones, the teeth, the blood, the lymph and chyle, the saliva, and sometimes in the urine. In all these situations it is normally in much smaller proportion than the calcareous phosphate with which it is associated. In the bones, however, it is next in importance to the lime phosphate, being on the average one-seventh as abundant as that salt, and much more so than any of the remaining mineral ingredients. In the animal fluids its solubility is accounted for by the presence of the alkaline chlorides or by that of free carbonic acid.

4. Magnesium Phosphate, $MgHPO_4$.

Magnesium phosphate was formerly associated with the corresponding lime salt under the name of the *earthy phosphates*, owing to certain resemblances in their chemical relations. Like the lime phosphate, which it everywhere accompanies, it is present in all the tissues and fluids of the body, though this substance is for the most part in the smaller quantity of the two. Thus in the bones the lime phosphate is in the proportion of 576 parts per thousand, while the magnesium phosphate forms only 12.5 parts. In the blood the calcareous salt amounts to 0.30 part per thousand, the magnesium salt to 0.22 part; and in the milk there are 2.72 parts of lime phosphate to 0.53 part of magnesium phosphate. On the other hand, the salts of magnesium have been found to be in larger quantity than those of lime in the muscles, and nearly twice as abundant in the substance of the brain.

The magnesium phosphate is discharged, by the urine, in the average daily quantity of 0.6 gramme. The average amount of both the earthy

phosphates, taken together, is accordingly about 1 gramme per day; the magnesian salt being rather the more abundant of the two.

Both the magnesium phosphate and carbonate, of which latter salt traces occur in the blood, appear to have similar physiological relations with the corresponding salts of lime, and almost the same things may be said in regard to their union with the substance of the more solid tissues and their mode of solubility in the animal fluids.

5. Sodium Chloride, NaCl.

This is undoubtedly the most important of the mineral constituents of the body, so far as regards its general distribution and the active part which it takes in the internal phenomena of nutrition. It is the most abundant of all, next to the lime phosphate, and it is universally present in all the animal tissues and fluids. Its entire quantity in the human body is estimated by Dr. Lankester at 110 grammes, or nearly one-quarter of a pound avoirdupois. In the blood it is rather more abundant than all the other mineral ingredients taken together. Its proportion in the various parts of the body is as follows:—

Quantity of Sodium Chloride in 1000 Parts in the

Bones	7.02	Saliva	1.53
Blood	3.36	Milk	0.30
Bile	3.18	Lymph	5.00
Gastric juice	1.70	Sebaceous matter	5.00
Perspiration	2.23	Urine	5.50

One of the most important characters of this salt in the living body is undoubtedly its property of regulating the phenomena of endosmosis and exosmosis, or the transudation of nutritive fluids through the organic membranes. This property is shared more or less by the other mineral ingredients of the blood, but is more important in the case of sodium chloride, owing to its preponderance in quantity as compared with the rest.

Since this substance is present in all parts of the body, it is also an important ingredient of the food. It occurs, of course, in all animal food, as a natural ingredient of the corresponding tissues. In muscular flesh, however, it is very much less abundant than potassium chloride, while, on the other hand, it is more abundant in the blood. It is present also in various articles of vegetable food.

According to Boussingault, it exists in the following proportions in certain vegetable substances:—

Proportion of Sodium Chloride in 1000 parts in

Potatoes	0.43	Oats	0.11
Beets	0.66	Peas	0.09
Turnips	0.28	Beans	0.06
Cabbage	0.40	Meadow hay	3.28

The relative quantity of sodium chloride taken in animal and vegetable food has not been determined. In regard to the demand for this salt,

however, there is a striking difference between the carnivorous and many herbivorous animals. The carnivora receive a fully sufficient supply with their natural food, and invariably show a repugnance to salt itself, as well as to salted meats. On the other hand, the horse, and more especially the ruminating animals, have an instinctive desire for salt, and greedily devour it, when offered to them, in addition to that naturally contained in the vegetable matters of their food. It is well known with what avidity the cattle, sheep, and all kinds of deer frequent the saline springs or "salt licks" of the United States; and it is shown by common experience that a liberal supply of salt is important for the healthy nutrition and development of these animals in the domesticated condition.

The same fact has been demonstrated in a more exact manner by the experiments of Boussingault on the ox.[1] This observer made a series of comparative investigations upon the growth of two sets of bullocks selected from animals of the same age and vigor, and supplied equally with an abundance of ordinary nutritious food, those of one set, however, receiving in addition each 34 grammes of salt per day. At the end of six months the difference in the aspect of the animals of the two sets began to be distinctly evident, and became more marked as time went on. The experiment lasted for a year, and at the end of that time both sets of animals had on the average equally increased in weight; but those fed with ordinary food alone presented a rough and tangled hide and a dull, inexcitable disposition, while in those which had received the additional ration of salt the hide was smooth and glistening and the general appearance was vigorous and animated. While these animals, therefore, may subsist for a time without inconvenience upon the salt naturally contained in their food, an additional quantity is required to maintain the system in good condition for an indefinite period.

There is a similar necessity for salt as an addition to the food of the human species. No other substance is so universally used as a condiment by all races and conditions of men. This custom does not depend simply on a fancy for gratifying the palate, but is based upon an instinctive demand of the system for a substance which is necessary for the full performance of its functions. Beside its other properties, it no doubt acts in a favorable manner by exciting the digestive fluids, and assisting in this way the solution of the food. For food which is tasteless, however nutritious it may be in other respects, is taken with reluctance and digested with difficulty; while the attractive flavor which is developed by cooking, and by the addition of salt and other condiments in proper proportion, excites the secretion of the saliva and gastric juice, and facilitates consequently the whole process of digestion. The sodium chloride is then taken up by absorption from the intestine, and is deposited in various quantities in different parts of the body.

[1] Chimie Agricole. Paris, 1854, p. 251.

Notwithstanding various surmises which have been presented from time to time with regard to its possible decomposition and the re-combination of its elements in the body, we have no certain knowledge of such changes taking place in the sodium chloride while forming a constituent of the animal frame. It passes from the alimentary canal to the blood, from the blood to the tissues, and is finally discharged with the urine, mucus, and cutaneous perspiration, in solution in the water of these fluids. Under ordinary circumstances, by far the largest proportion passes out by the kidneys. The quantity of sodium chloride thus discharged with the excretions by an adult man is about 15 grammes per day;[1] of which 13 grammes are contained in the urine, and 2 grammes in the perspiration. Thus, of all the sodium chloride contained in the body, considerably more than ten per cent. passes through the system in twenty-four hours. This fact plainly indicates the activity and importance of this salt in the daily internal changes of nutrition.

6. Potassium Chloride, KCl.

This substance is found in very many if not all of the animal tissues and fluids, accompanying the sodium chloride, many of the properties of which it shares, and with which it is closely related in its physiological characters. It is especially abundant, as compared with the sodium chloride, in the muscles and in the milk, less so in the blood, the gastric juice, the urine, and the perspiration. Both salts are neutral in reaction, and are retained in the liquid form in the blood and secretions by solution in the water of these fluids. The potassium chloride is introduced as an ingredient of both animal and vegetable food, and is discharged with the mucus, the urine, and the perspiration.

7. Sodium and Potassium Phosphates, Na_2HPO_4 and K_2HPO_4.

These substances, associated under the name of the *alkaline phosphates*, are of the greatest importance as ingredients of the animal body. They exist universally in all its solids and fluids, and in the latter are present in the liquid form by means of their ready solubility in water. No doubt they are useful in a variety of ways, but at least one of their most important characters is their property of exhibiting an alkaline reaction. This reaction is essential to a large number of the vital processes taking place in the interior, and is present, without exception, in all the animal fluids which are actually contained in the circulatory system, or in the closed cavities of the body. An acid reaction, on the other hand, is found only in a very few of the organic fluids which are either employed in the process of digestion or are discharged externally.

The following list shows the comparative frequency of alkaline and acid reactions in the animal fluids :—

[1] Neubauer und Vogel, Analyse des Harns, Wiesbaden, 1872, p. 54. Beneke, Pathologie des Stoffwechsels, Berlin, 1874, p. 322.

Fluids with an Alkaline Reaction.	Fluids with an Acid Reaction.
1. Blood-plasma.	1. Gastric juice.
2. Lymph.	2. Perspiration.
3. Aqueous humor.	3. Mucus of the vagina.
4. Cephalo-rachidian fluid.	4. Urine.
5. Pericardial fluid.	
6. Synovia.	
7. Fluids of the living muscular tissue.	
8. Mucus in general.	
9. Milk.	
10. Spermatic fluid.	
11. Tears.	
12. Saliva.	
13. Pancreatic juice.	
14. Intestinal juice.	

If we take into account the carbonic acid exhaled with the breath, we see therefore that, while in general an alkaline condition is characteristic of the internal fluids, the products of excretion, on the contrary, present universally an acid reaction.

Of all the internal fluids the most essential is the plasma of the blood, since it affords the materials of nutrition to the entire system; and its alkaline reaction, which is distinctly marked, has been found to be invariably present, not only in the human subject, but also in every species of animal in which it has been examined. This reaction of the blood is moreover necessary to life, since Bernard has shown[1] that if an injection of dilute acetic or lactic acid be made into the veins of the living animal death always results before the point of neutralization has been reached.

The alkaline reaction of the blood-plasma gives to this fluid its extraordinary capacity for dissolving carbonic acid. According to Liebig, water which holds in solution one per cent. of sodium phosphate is enabled to absorb and retain twice its usual proportion of carbonic acid; and the other alkaline salts, as is well known, have a similar dissolving action upon this gas. Consequently the blood as it circulates among the tissues rapidly absorbs from them the carbonic acid which has been formed in their substance, and incessantly carries it away to be eliminated by the lungs. This important property of the circulating fluid depends upon its alkaline reaction.

The alkalescence of the blood is due in great measure to the alkaline phosphates, which are present in human blood in the proportion of 0.67 per thousand parts. A peculiar relation, however, exists in this respect, for different classes of animals, between the alkaline phosphates and the alkaline carbonates, which are to be mentioned hereafter. Both these groups of salts have, when in solution, an alkaline reaction; and both contribute to the alkalescence of the blood in man and animals. But in the carnivorous animals it is the phosphates which preponderate, while

[1] Liquides de l'Organisme. Paris, 1859, tome i. p. 412.

in the herbivora the carbonates are the more abundant of the two. In animals fed at the same time upon both animal and vegetable food the two kinds of salts are found to be present in nearly equal proportion, and in the same animal either the phosphates or the carbonates may be made to predominate by increasing the relative quantity of animal or vegetable food respectively. This is readily understood when we remember that muscular flesh and the animal tissues generally are comparatively abundant in phosphates, while vegetable matters, as we shall hereafter see, abound also in salts of the organic acids, which give rise by their decomposition in the system to carbonates of the same bases.

The alkaline phosphates are taken in with the food, as they exist widely in both animal and vegetable matters. They circulate with the animal fluids, and are finally excreted with the perspiration, the mucus, and the urine. In the urine a portion of the alkaline sodium phosphate is replaced by the acid sodium biphosphate, which gives to this fluid its property of reddening blue litmus paper, although it contains no free acid. The manner in which this change is supposed to take place is the following. A nitrogenous organic acid of new formation, namely, uric acid, makes its appearance in the system, and is excreted by the urine. It exists, however, in this fluid only in the form of combination, as sodium urate. It is, therefore, believed to combine, at the time of its formation, with a portion of the sodium which forms the base of the sodium phosphate; and the remainder of this salt, converted into a biphosphate, is then eliminated by the urine, which thus acquires an acid reaction.

There is evidence that phosphoric acid is also generated in the interior of the body by oxidation. A substance to be described hereafter, containing phosphorus in the form of organic combination, exists in various parts of the system, especially in the blood and in the tissue of the brain and nerves, and is taken with certain kinds of food; but no such substance is to be met with in the excretions. In the fluids discharged from the body phosphorus exists only in the form of the phosphatic salts. It is, therefore, without doubt oxidized in the internal transformation of the organic substances, thus becoming phosphoric acid, which in turn unites with the alkaline bases to form neutral or acid phosphates. In this way a certain portion of the superabundant acid is produced, which gives rise to the acid reaction of the excreted fluids.

The sodium and potassium phosphates, including the acid biphosphate, are discharged with the urine to the amount of about 4.5 grammes per day.

8. Sodium and Potassium Carbonates, Na_2CO_3 and K_2CO_3.

The alkaline carbonates, as mentioned above, are associated with the phosphates in all the more important fluids of the body. They are readily soluble, and assist in producing the necessary alkalescence of the blood and secretions.

The alkaline carbonates are partly introduced as such with the food, but are to a great extent formed within the body by the decomposition of other salts contained in the substance of certain fruits and vegetables. Various of these fruits and vegetables, such as apples, cherries, grapes, potatoes, carrots, and the like, contain malates, tartrates, and citrates of the alkaline bases. It has, furthermore, been often observed that after the use of acescent fruits and vegetables containing the above salts, the urine becomes alkaline in reaction from the presence of the alkaline carbonates. Lehmann[1] found, by experiments upon his own person, that within thirteen minutes after taking 15.5 grammes of sodium lactate, the urine had an alkaline reaction. He also observed that, if a solution of this substance were injected into the jugular vein of a dog, the urine became alkaline at the end of five, or, at the latest, of twelve minutes. The conversion of these salts into carbonates takes place, therefore, not in the intestine, but in the blood. The same observer found that, in many persons living on a mixed diet, the urine became alkaline in two or three hours after swallowing 0.65 gramme of sodium acetate.

The organic acid in these cases is decomposed and oxidized with the production of carbonic acid and water; and the original salts are thus replaced by the alkaline carbonates, which appear in the urine and temporarily modify its reaction in the manner above described.

A preponderance of vegetable food, accordingly, influences the quantity of the alkaline carbonates in the system, and consequently the reaction of the excretions. As a rule, the urine of man and of the carnivorous animals is clear and acid, while that of the herbivora is alkaline and turbid with calcareous deposits. This turbid and alkaline urine will often effervesce with acids, showing the presence of carbonates in considerable quantity. Bernard has shown that this difference depends upon the alimentation of the animal, and that although in carnivorous and herbivorous animals under ordinary conditions the urine is respectively acid and alkaline, if they be both deprived of food for a few days the urine becomes acid in both, since they are then, in each instance, living upon their own tissues. Furthermore, a rabbit, whose urine is turbid and alkaline while feeding on fresh vegetables, if kept upon a diet of animal food, soon produces an excretion which is clear and acid. The reverse effect is produced upon a dog by changing his food from meat to vegetable matters. Finally, it is also shown[2] that the urine of the young calf while living on the milk of the mother is clear and acid; but after the animal has been weaned and feeds upon vegetable matter, its urine becomes alkaline and turbid, like that of the adult animal.

9. Sodium and Potassium Sulphates, SO_4Na_2 and SO_4K_2.

The sulphates are also to be regarded as constant ingredients of the body, as they are found in several of the animal fluids, including the

[1] Physiological Chemistry. Cavendish edition. London, 1851, vol. i. p. 97.

[2] Milne Edwards, Leçons sur la Physiologie. Paris, 1862, tome vii. p. 471.

blood, the lymph, the aqueous humor, milk, saliva, mucus, the perspiration, and the urine. They are usually, however, in small quantity, as compared with other saline matters. In the blood and the lymph, they are much less abundant than either the chlorides, phosphates, or carbonates. In the milk and the saliva, there is hardly more than a trace of them; and they have not been found at all in the bones, the gastric juice, the bile, or the pancreatic juice. They are most abundant in the urine, where they amount to rather more than one-half the quantity of the phosphates, and they are found also, in small proportion, in the feces.

The sulphates are introduced into the body, to some extent, with the food and drink. They are to be found, in minute quantity, in muscular flesh and in the yolk of egg. They exist also in certain vegetable products, such as the cereal grains, fruits, and tuberous roots, where they are much less abundant than the phosphates, though often more so than the chlorides. Spring and river water, as used for drink, usually contains sulphates, including sulphate of lime, varying in amount, according to the tables given by Payen,[1] from .003 to .06 per thousand parts. In the water of the Croton River, with which the city of New York is supplied, they amount, as shown by the analyses of Prof. Chandler,[2] to a little more than .007 per thousand parts.

Beside the sulphates, however, introduced with the food and drink, a certain amount of sulphuric acid originates within the body by oxidation, in a mode analogous to that already described for phosphoric acid. The albuminous substances, which form so important a part of the solid food, contain sulphur as one of their constituent elements, and a considerable quantity of this substance is accordingly introduced daily into the system in the form of organic combination. The entire quantity of sulphur, thus forming part of the organic matters of the body of a man of medium size, amounts, according to Payen,[3] to about 110 grammes; and at least 1 gramme must be taken daily with the albuminous ingredients of the food. A portion of these substances is expelled by the daily exfoliation of the hair, nails, and epidermis; but no such sulphurous organic compound is discharged by the urine and feces except in insignificant quantity. On the other hand, the sulphates are comparatively abundant in the excretions. While they are to be found in the blood only in the proportion of 0.28 per thousand, they exist in the urine in the proportion of from 3.00 to 7.00 parts per thousand,[4] and are discharged by this channel to the amount of about 4 grammes per day.

These facts indicate that a notable quantity of sulphuric acid is constantly formed in the body, during the decomposition of albuminous matters, by oxidation of their sulphur. This is confirmed by the fact that the quantity of sulphuric acid in the sulphates eliminated by the kidneys is perceptibly increased by the use of a flesh diet, and also by

[1] Substances Alimentaires. Paris, 1865, p. 436.
[2] Lecture on Water. Transactions of the American Institute for 1870–71.
[3] Substances Alimentaires. Paris, 1865, p. 68.
[4] Robin, Leçons sur les Humeurs. Paris, 1874, p. 770.

the administration of sulphur or a sulphuret.[1] Dr. Parkes estimates the quantity of sulphuric acid thus produced in the system as about double that taken in the form of sulphates with the food and drink. It unites at once with the alkaline bases, displacing the weaker acids with which they were previously combined, and thus contributes indirectly to the general acid reaction of the excreted fluids.

The foregoing substances constitute the most important of the inorganic proximate principles of the animal body. They are distinguished, as a class, by their comparatively simple chemical composition, by their external origin, and by the part which they take in the constitution and nourishment of the animal frame They are derived for the most part from without, being taken directly from the materials of the inorganic world. There are some exceptions to this rule; as in the case of the alkaline carbonates formed in the body by decomposition of the salts of the vegetable acids; and of the sodium biphosphate produced from the neutral phosphate, by the action of an organic acid of internal origin. The greater part, however, of the proximate principles belonging to this class are introduced with the food, and taken up by the animal tissues and fluids, in the form under which they exist in external nature. The lime carbonate of the bones, for example, and the sodium chloride of the blood and the tissues, are the same substances as those met with in calcareous rocks, or in solution in sea water.

In the process of internal nutrition they are also exempt, as a general rule, from any marked chemical changes. Some of them, such as the lime and magnesium phosphates, are mostly deposited in the solid parts, and are renewed very slowly, contributing principally to the physical properties of the tissues, and taking a comparatively small share in the actions of repair and waste. Others, such as water and the alkaline chlorides, are introduced and discharged daily in considerable abundance, passing rapidly through the system, and playing an important part in the phenomena of solution and transudation. Others still, such as the alkaline phosphates and sulphates, are partly formed in the body by the process of oxidation, and appear in the urine as a residue from the decomposition of other proximate principles.

Principally, however, the inorganic substances are reabsorbed by the blood from the tissues in which they were deposited, and discharged unchanged with the excretions. The importance of this character will become fully manifest when we see how different are the relations exhibited by the proximate principles of other groups. The inorganic substances do not, for the most part, participate directly in the chemical changes going on in the body; but rather serve by their presence to enable those changes to be accomplished, in the other ingredients of the animal frame, which are necessary to the process of nutrition.

[1] Neubauer und Vogel, Analyse des Harns. Wiesbaden, 1872, pp. 356, 357.

CHAPTER III.

HYDROCARBONACEOUS PROXIMATE PRINCIPLES.

THE proximate principles belonging to this class are distinguished from the preceding by their organic origin. They appear as products of the nutritive actions of organized beings, and are not introduced ready formed from the inorganic world. They exist both in vegetables and in animals. In the former they are produced entirely as new combinations, under the influence of the vegetative process; and even in animals, which feed upon vegetables or upon other animals, they are so modified by digestion and assimilation that they present themselves, as final constituents of the body, under new and specific forms. They all consist of carbon, hydrogen, and oxygen, of which carbon is present by weight in especially large proportion, forming from 44 to 84 per cent. of the entire substance. Owing to the absence of nitrogen, which is an important element in organic substances of the following class, they are sometimes known as the "non-nitrogenous" proximate principles. They are naturally divided into two principal groups, namely: the *carbohydrates*, or substances containing carbon, together with hydrogen and oxygen in the proportions to form water; and the *fatty matters*, in which the proportions of carbon and hydrogen are both increased, while that of oxygen is considerably diminished. The group of the carbohydrates includes starch, glycogen, and sugar.

I. Starch, $C_6H_{10}O_5$.

Starch is most abundantly diffused throughout the vegetable kingdom, and exists, for at least a certain period of vegetative life, in every plant which has yet been examined for it. It occurs especially in seeds, in the cotyledons of the young plant, in roots, tubers, and bulbs, in the pith of stems, and sometimes in the bark. It is very abundant in corn, wheat, rye, oats, and rice, in the parenchyma of the potato, in peas and beans, and in most vegetable substances used as food. It constitutes almost entirely the different preparations known as sago, tapioca, arrowroot, and maizena, which are nothing more than varieties of starch, extracted from different species of plants.

The following list, compiled mainly from the tables of Payen,[1] shows the percentage of starch occurring in various kinds of food:—

[1] Substances Alimentaires. Paris, 1865.

QUANTITY OF STARCH IN 100 PARTS IN

Wheat	57.88	Potatoes	20.00
Rye	64.65	Sweet potatoes	16.05
Oats	60.59	Peas	37.30
Barley	66.43	Beans	33.00
Indian corn	67.55	Flaxseed	23.40
Rice	88.65	Chocolate nut	11.00

When purified from foreign substances starch is a white, glistening powder, which gives rise to a peculiar crackling sensation if rubbed between the fingers. It consists of minute granules of very firm consistency and definite shape, presenting certain peculiarities, of both form and size, by which its varieties, derived from different sources, may be distinguished from each other. The young starch granules, when first produced in the tissues of the plant, are exceedingly small, round, and perfectly homogeneous; but they afterward increase in size, and, as their growth is irregular, they become ovoid, pear-shaped, lenticular, or polygonal in form. They also show under the microscope a definite structure, each granule being composed of a series of layers, disposed one over the other, giving rise to the appearance of concentric markings, which are very characteristic of most varieties of starch grains, after they have attained a certain size. The markings are arranged round a single point, usually more or less eccentric in position, which is called the *hilum.*

The successive layers of which the starch granule is composed differ from each other mainly in their consistency, being alternately harder and softer in comparison with each other; and this difference in density produces a corresponding difference in the refractive power of the layers, and consequently an appearance of concentric striation.

Fig. 2.

GRAINS OF POTATO STARCH.

Each starch granule, furthermore, consists of two substances, intimately mingled in every part of its mass, which resemble each other completely in chemical composition, but differ greatly in solubility. These two substances are, 1st, *granulose*, which may be extracted from the starch grain by boiling water; and 2d, *cellulose*, which remains undissolved. The granulose is usually much the more abundant of the two, but the cellulose has so marked a consistency that it retains the form and apparent laminated structure of the starch grain,

after extraction of the granulose, though it may be reduced to five or six per cent. of its original weight.

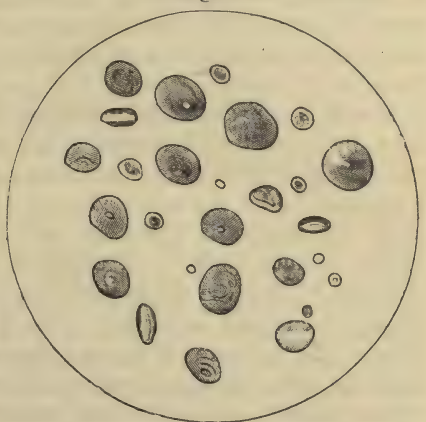
The starch grains of the potato (Fig. 2) vary considerably in size. The smallest have a diameter of 2.5 mmm.,[1] the largest 62.5 mmm. They are irregularly pear-shaped in form, and their concentric markings are very distinct. The starch obtained from the potato, however carefully prepared, retains in connection with it traces of an odoriferous principle which makes it less valuable for culinary purposes than many other varieties.

Fig. 3.

STARCH GRAINS OF BERMUDA ARROW-ROOT.

The starch granules of arrowroot (Fig. 3) are generally smaller and more uniform in size, than those of the potato. They vary from 12.5 mmm. to 50 mmm. in diameter. They are elongated and cylindrical in form, and the concentric markings are less distinct than in the preceding variety. The hilum has here sometimes the form of a circular pore, and sometimes that of a transverse fissure or slit.

Fig. 4.



STARCH GRAINS OF WHEAT FLOUR.

The grains of wheat starch (Fig. 4) are still smaller than those of arrowroot. They vary from 2.5 mmm. to 35 mmm. in diameter. They are nearly circular in form, with a round or transverse hilum, but without any distinct appearance of lamination. Many of them are flattened or compressed laterally, so that they present a broad surface in one position, and a narrow edge when viewed in the opposite direction.

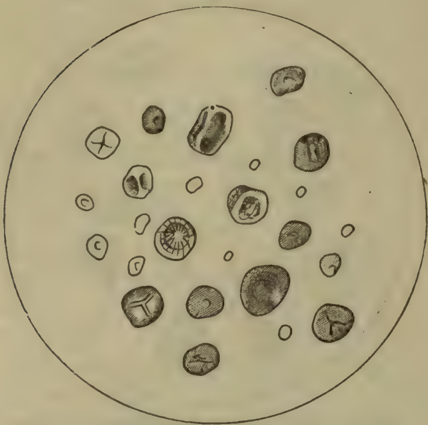
The starch grains of Indian corn (Fig. 5) are of nearly the same size with those of wheat flour. They are somewhat more irregular and angular in shape; and

[1] The sign mmm. stands for *micro-millimetre;* that is, the one-thousandth part of a millimetre. A millimetre is very nearly equivalent to one twenty-fifth of an inch; and a micro-millimetre, accordingly, is about $\frac{1}{25000}$ of an inch.

are often marked with crossed or radiating lines, as if from partial fracture.

Starch derived from all these different sources has essentially the same chemical composition, and may be recognized by the same tests. It is insoluble in cold water, but if it be treated with about twenty times its weight of boiling water its granules swell, become gelatinous and amorphous, combine with a certain proportion of water, and fuse into a thick opaline liquid, which is thinner or thicker according to the quantity of water present. After that they cannot be made to resume their original form, but on cooling they solidify into a nearly homogeneous paste, retaining the water in union with the starchy matter. The starch is then said to be amorphous or "hydrated." By this process it is not essentially altered in its chemical properties, but only in its physical condition. If starch be treated with 100 or 150 parts of boiling water, it makes an opaline liquid which does not gelatinize; but on standing, the imperfectly liquefied portions, containing the insoluble cellulose, subside to the bottom as a turbid deposit, while the soluble starch remains above, forming a clear, colorless, and perfectly fluid solution.

Fig. 5.



STARCH GRAINS OF INDIAN CORN.

Starch is especially distinguished by its property of striking a blue color by contact with iodine. This reaction will take place even when the starch is in the raw condition, and starch granules may be readily recognized under the microscope by this means. It is still more prompt when the starch is hydrated and especially when it is in solution. A very minute quantity of tincture of iodine added to a solution of starch will cause the whole to assume at once a very deep and rich blue color, which may be largely diluted without losing its characteristic tinge. The mixture of the two substances, however, must, in the first place, be made at a moderate temperature. If the solution be hot, no visible reaction will occur; and even after it has taken place if heat be applied the blue color will disappear, to return again after cooling down to the original temperature. Secondly, the iodine must be in a free state. If it be used in the form of a soluble iodide, it will produce no effect, since the starch has not sufficient affinity for it to withdraw it from its union with other matters. No third substance, furthermore, must be present in the mixture, which would be capable of combining with the iodine and thus preventing its action upon the starch. All the

animal fluids more especially, such as the serum of blood, saliva, mucus, urine, contain ingredients which prevent the reaction of starch with iodine, and may even dissipate the blue color after it has been once produced. These substances, therefore, must be removed from the fluid before the application of the test, or else the iodine must be added in sufficient excess to allow a surplus for action upon the starch. With these precautions it forms a striking and valuable test.

Starch has the property of being changed, under certain conditions, into two other substances.

1. If subjected to torrefaction, that is, a dry heat of about 210° (about 400° F.), it is converted into *Dextrine*, a gummy substance freely soluble in water, so called from the fact that in solution it rotates the plane of the polarized ray toward the right.[1] Dextrine has the same chemical composition with starch, namely $C_6H_{10}O_5$, but its properties are changed, and it will no longer produce a blue color with iodine. The same transformation is very quickly accomplished by boiling starch with a dilute acid; the opaline and gelatinous solution becoming in a few minutes clear and liquid, and losing at the same time its power of reaction with iodine. Finally, in the germination of starchy seeds, like the cereal grains, a nitrogenous substance is produced termed "diastase;" and this has the power, when supplied with moisture at a moderate temperature, of effecting the transformation of the starch into soluble dextrine.

2. Starch may be converted into *Sugar*. When a starch solution or a thin starch paste is boiled with a dilute acid, it is rapidly changed, as already mentioned, into dextrine. If the boiling be continued for several hours it is still further transformed into sugar; and at last the whole of it passes over into the saccharine condition. This also happens in the process of germination and growth in plants, where sugar makes its appearance under influence of the diastase, and at the expense of the starch, as soon as moisture and warmth are supplied in the requisite degree. This is the usual source of sugar in vegetable

[1] A ray of light which has passed through certain crystalline bodies, such as a "Nicol's prism" of Iceland spar, is found to be *polarized;* that is, it has acquired opposite and complementary properties in two different directions. For if it be received by a second similar prism, which is equally transparent in all positions to ordinary light, the polarized ray will pass through it only when the principal section of the second prism is parallel with that of the first; but when the second prism is turned round 90°, the light is entirely arrested. Now if certain organic substances in solution be placed between the two prisms, it is found that they have the effect of changing the angle at which the second prism must stand in order to arrest or transmit the light from the first. In other words, the plane of polarization of the polarized ray has been deviated or rotated by passing through the organic liquid. Some substances deviate in this way the plane of polarization toward the right, others toward the left. The specific rotatory power of each is estimated for a solution of standard strength and quantity, for yellow light, and is indicated in degrees of the circle. The specific rotatory power of dextrine is 118°.

juices, the starch previously stored up being at some period of growth changed into sugar by the molecular actions going on in the vegetable fabric. Finally, various nitrogenous animal substances produce the same effect. The contact of human saliva or the intestinal juices at a temperature of 37.5° (100° F.) rapidly transforms hydrated starch into sugar.

A special interest attaches to starch from the fact that it is the first organic substance produced, in the process of vegetation, from inorganic materials. The animal body is incapable of forming organic matter, and must therefore be supplied with these substances in the food. But vegetables have the power of combining inorganic elements in such a way as to produce a new class of bodies, peculiar to the organic world, and capable of serving for the nutrition of animals. This is shown by numerous experiments, in which seeds or young plants, artificially cultivated in a soil of clean sand, and moistened only with solutions of various mineral salts,[1] have germinated, grown, and fructified, increasing, many times over, the quantity of organic material which they contained at the beginning.

This production of organic matter takes place in the green tissues, principally in the leaves, of growing plants, under the influence of the solar light; and the first substance which makes its appearance under these conditions is nearly always starch. It is produced from two inorganic matters absorbed from without, namely, carbonic acid and water, which are deoxidized by the green vegetable tissues, their elements being re-combined, to form a carbo-hydrate. This is proved by the fact that oxygen is exhaled, during the vegetative process, in the same or nearly the same proportion as that in which it existed originally in the carbonic acid; and the new substance produced contains hydrogen and oxygen in the relative proportions to form water. The production of starch in growing vegetables is therefore represented by the following formula:—

$$\underset{\text{Carbonic acid.}}{(C_6O_{12}} + \underset{\text{Water.}}{H_{10}O_5)} - O_{12} = \underset{\text{Starch.}}{C_6H_{10}O_5}.$$

The starch thus formed in the leaves of plants is afterward transformed into other vegetable substances belonging to the group of the carbo-hydrates, such as dextrine, sugar, and cellulose, and used for the further nutrition of the plant. When abundantly deposited in special organs, such as the starchy seeds of wheat or Indian corn, or the tubers of the potato, it constitutes a reserve material of nutrition, to be afterward dissolved and employed for the purposes of germination and growth. It is from such natural deposits of reserve, in the vegetable fabric, that starch is obtained in quantity to serve as food for animals or man.

[1] Mayer, Lehrbuch der Agrikultur-Chemie. Heidelberg, 1871, Band i. p. 10.

When taken into the alimentary canal, starch is rapidly transformed into sugar by the action of the digestive fluids; and in this form is absorbed into the circulation.

II. Glycogen, $C_6H_{10}O_5$.

This is an amylaceous substance of animal origin, corresponding in character with starch derived from the vegetable world. It is found in the livers of all vertebrate animals in the healthy condition, and in the muscles and integument of the embryo of mammalia at an early period of development. It has also been discovered in the oyster and the cockle-shell. Glycogen, so called from its property of producing sugar or glucose, has the same chemical composition as starch, and agrees with it in all its essential characters, except that it is readily soluble in water, and, when treated with iodine, yields a violet-red instead of a blue color. Its watery solution is opalescent, and deviates the plane of polarization strongly to the right, its specific power of rotation for yellow light being about 130°. By boiling with a dilute acid it is changed first into dextrine and afterward into sugar. It also undergoes the saccharine transformation when in solution at the temperature of the living body by contact with saliva, the intestinal juices, the substance of the liver, or the serum of the blood. It is the source of the sugar produced in the animal body, as starch is the source of that formed in vegetables.

Both starch and glycogen, accordingly, are to be regarded as temporary products, destined to undergo further transformation before being used for the purposes of nutrition. In vegetables, the starch which is abundantly stored up at one period in the cellular tissues is afterward liquefied and altered into other substances; and although it enters so largely into the composition of the vegetable food of animals, it is converted into sugar during digestion in the alimentary canal.

III. Sugar.

The proximate principles designated under this name include a variety of substances which have certain well-marked characters, and are of frequent occurrence in both animal and vegetable juices. They are crystallizable and soluble in water, and have, when in solution, a distinctly sweet taste, which, in some varieties, is very highly developed. They are all decomposed by being heated with sulphuric acid; their hydrogen and oxygen being driven off, while the carbon remains behind as a jet-black deposit. In this condition they are said to be carbonized. The proportions in which they occur in various articles of food, according to the tables of Payen, Von Bibra, and a few other observers, are as follows:—

QUANTITY OF SUGAR IN 100 PARTS IN

Cherries	18.12	Wheat flour	2.33
Apricots	16.48	Rye flour	3.46
Peaches	11.61	Barley meal	3.04
Pears	11.52	Oat meal	2.19
Juices of sugar-cane	18.00	Indian corn meal	3.71
Sweet potatoes	10.20	Cow's milk	5.20
Beet roots	8.00	Goat's milk	5.80
Parsnips	4.50	Beef's liver	1.79

The three principal varieties of this substance which are most important in a physiological point of view are glucose, cane sugar, and milk sugar.

Glucose, $C_6H_{12}O_6$.

Glucose, also called *grape sugar* from its abundance in the juices of the ripe grape, may be considered as the most marked and representative variety of the saccharine substances. It occurs more frequently than any other in the animal fluids, being found in the juices of the liver, in the chyle, the blood, and the lymph. In diabetes it is abundantly excreted with the urine. It is also found in the juices of many plants, in various sweet fruits, and in honey, where it is associated with certain other varieties. It is freely soluble in water. Its solution has a moderately sweet taste, and deviates the plane of polarization toward the right 53.5°.

It is this form of sugar which is produced from starch by boiling with dilute acids, by the action of the digestive fluids of the alimentary canal, and in the plant during the process of vegetation. The change consists in the assumption by starch of the elements of water in due proportion, the new substance thus produced being still a carbo-hydrate. The transformation of starch into glucose is therefore represented as follows:—

$$\underset{\text{Starch.}}{C_6H_{10}O_5} + \underset{\text{Water.}}{H_2O} = \underset{\text{Glucose.}}{C_6H_{12}O_6}.$$

Glucose may be recognized in solution by various well-marked tests. First, the *action of alkalies at a boiling temperature.* If a solution of glucose be treated with a solution of potassium hydrate and heat applied, the sugar is decomposed and the liquid assumes, first, a yellowish and then a brown color, which becomes deeper in proportion to the amount of glucose and alkali existing in the solution. This is not a certain test for the presence of glucose, as some other organic matters are discolored in a similar way by the strong alkalies; but it will serve to distinguish it from certain varieties of sugar, which do not possess this property.

Secondly, the test most commonly employed for detecting glucose depends upon its power of *reducing the salts of copper in a boiling alkaline solution.* This test, which is known as "Trommer's test," is applied in the following manner: A very small quantity of copper sulphate in solution should be added to the suspected liquid, and the

mixture then rendered distinctly alkaline by the addition of potassium hydrate. The whole solution then takes a deep-blue color. On boiling the mixture, if sugar be present, the copper suboxide is thrown down as an opaque red, yellow, or orange-colored deposit; otherwise no change of color takes place. In this reaction the sugar, which is oxidized at a high temperature under the influence of the alkali, takes a portion of its oxygen from the copper in the copper salt, and thus reduces it to the form of an insoluble suboxide.

Some precautions are necessary in the use of this test. As a general rule, only a small quantity of the copper sulphate should be added to the liquid under examination, just sufficient to give to the whole a distinct blue tinge after the addition of the alkali. If the copper salt be used in excess, the sugar in solution may not be sufficient to reduce the whole of it; and that which remains as a blue sulphate may mask the yellow color of that which is thrown down as a deposit. This difficulty may be removed by due care in the proportion of the ingredients.

Furthermore, there are some albuminous substances which have the power of interfering with Trommer's test, and prevent the reduction of the copper even when sugar is present. Certain animal matters, to be more particularly described hereafter, which are liable to be held in solution in the gastric juice and in the blood, have this effect.

The ordinary ingredients of the urine also interfere with the complete reaction of Trommer's test, by holding the copper oxide in solution, so that no precipitate takes place when glucose is present, although the liquid turns yellow on boiling. A very large proportion of glucose may be added to fresh urine without giving rise to a pulverulent precipitate on the application of Trommer's test; notwithstanding that, if dissolved in water, it will react in the proportion of one part in 10,000. That the interference of urine with Trommer's test depends on its retaining in solution the reduced copper oxide, and not upon its preventing deoxidation, is indicated by the fact that the color of the mixture changes, as usual, from blue to yellow although no precipitate takes place; and also by the experiments of Dr. Fowler,[1] who has shown that if the precipitate resulting from Trommer's test with a watery solution of glucose be added to boiling urine, it is at once redissolved. The same observer has devised a method of applying the test successfully notwithstanding the interference of the urine. A certain quantity of urine can, of course, only dissolve a certain amount of copper oxide; and if the copper sulphate solution be added to a specimen of saccharine urine in large proportion, the excess will be precipitated and show itself as a deposit. A copper sulphate solution, made in the proportion of 1 part copper sulphate to 7.5 parts of water, and added to saccharine urine to the amount of one-half or one-third its bulk will generally be sufficient to produce a satisfactory reaction.

[1] New York Medical Journal, June, 1874, p. 632.

All sources of error of this kind, due to the presence of extraneous substances, may be avoided in delicate examinations, by treating the suspected fluid with animal charcoal, or by evaporating it to dryness, extracting the dry residue with alcohol, and then dissolving the dried alcoholic extract in water, before the application of the test. Either of these processes will remove the substances which interfere with the action of Trommer's test, and will leave the glucose by itself in the watery solution.

A more delicate form of the copper test for glucose is in the employment of "Fehling's liquor," which is an alkaline solution of a double copper and potassium tartrate. It is made as follows:—

Take—Pure crystallized copper sulphate	40 grammes.
Neutral potassium tartrate	160 "
A solution of sodium hydrate of the specific gravity 1.12 .	650 "

The neutral potassium tartrate, dissolved in a little water, is first mixed with the solution of sodium hydrate. Then the copper sulphate, dissolved in 160 cubic centimetres of water, is gradually added to the alkaline liquor, which assumes a clear, deep blue color. The whole is finally diluted with water to the volume of 1154.4 cubic centimetres. If one drop of this liquid be added to one cubic centimetre of a saccharine solution and heat applied, it will detect one-fifteenth of a milligramme of glucose by the reduction of the copper oxide. One advantage of Fehling's liquor as a test is that the quantity of copper salt contained in a given volume is accurately known, and consequently not only the presence but also the amount of glucose in any solution may be determined by the quantity of test liquid which it decomposes at a boiling temperature. One cubic centimetre of Fehling's liquor is exactly decolorized by $\frac{1}{200}$th of a gramme of glucose.

One inconvenience connected with this test is that Fehling's liquor by exposure to the air and light undergoes an alteration, in which some of its tartaric acid disappears and is replaced by carbonic acid. In this condition it will partially precipitate on boiling, even without the presence of sugar. To guard against this, it should be kept in bottles which are quite full and protected from the light; and, in every case where a suspected fluid is to be examined for sugar, a small portion of the test-liquor should be previously boiled by itself, in order to be sure that it has not undergone spontaneous decomposition. Although by exposure to the air and light at a summer temperature, Fehling's liquor may become altered at the end of a week, yet if protected from the light, in carefully closed and full bottles, it can be kept unchanged for two or three years.

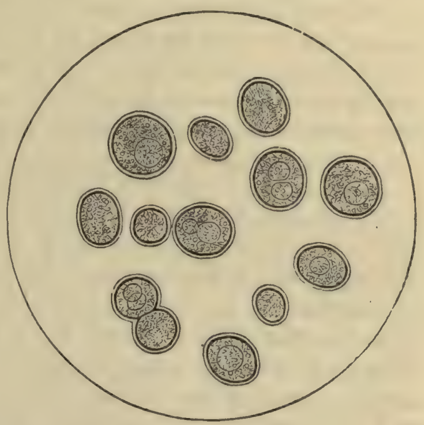
Thirdly, the most marked and distinctive property of glucose, in a physiological sense, is its capacity for *fermentation*. If a watery solution of pure glucose be left to itself, even exposed to the air, no remarkable change takes place in it. But if a small quantity of beer-yeast be added and the mixture kept at a temperature of about 25° (77° F.), after a short time it becomes turbid. It then develops an abundance of

carbonic acid, which is partly dissolved in the liquid and partly rises in the form of gas bubbles to its surface. It is this circumstance which has given to the process the name of "fermentation" or boiling. At the same time the sugar is gradually destroyed and alcohol appears in its place. Finally the whole of the glucose is decomposed, having been converted principally into alcohol, C_2H_6O, and carbonic acid, CO_2. Then the fermentation stops and the liquid becomes clear, its turbid contents subsiding to the bottom as a whitish layer. This layer is itself found to consist of yeast, which has increased in quantity over that originally added, and is itself capable of exciting fermentation in another saccharine liquid.

If, instead of a solution of pure glucose, we employ the expressed juices of certain fruits, like those of the grape, which contain nitrogenous albuminoid matters in addition to glucose, fermentation begins after a certain period of exposure to the air, and goes on with the same phenomena and results as before. This is the natural source of all the vinous and alcoholic fluids used by man; namely, the fermentation of some fluid containing glucose or a similar saccharine substance.

The alcoholic fermentation of glucose is due to the vegetative action of a microscopic fungus, known as *Saccharomyces*. This plant consists entirely of cells which multiply by a process of budding, but do not produce filaments, nor any compound vegetable fabric. The species which is present in beer-yeast is the "Saccharomyces cerevisiæ." Its cells are usually rounded in form, sometimes oval (Fig. 6). They vary in size, but the greater number have an average diameter of 10 mmm. They have a very thin investing integument, which incloses a finely granular semi-solid substance, often with one or two rounded cavities or vacuoles filled with fluid. The cells are mostly isolated, but occasionally two of them may be seen adhering to each other. There is also a small amount of intercellular liquid, containing albuminous matter and various mineral salts.

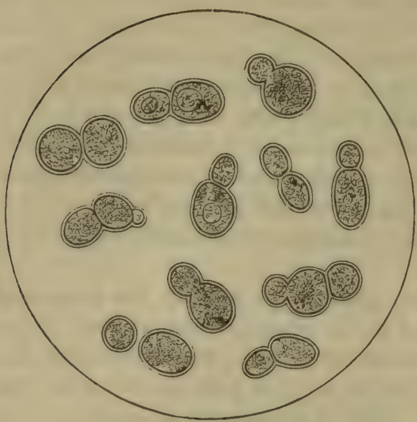
Fig. 6.



Saccharomyces Cerevisiæ, in its quiescent condition; from deposit of beer-yeast, after fermentation.

When a little of the yeast is added to a solution containing glucose, the cells of the yeast-plant after a short time begin to multiply by budding. The buds increase rapidly in size, and, when the young cell has nearly attained the size of its parent, it usually separates and begins an

Fig. 7.



SACCHAROMYCES CEREVISIÆ during active germination. From fermenting saccharine solution.

independent existence. While in this active condition the cells are mostly oval in form, and have an average diameter of only a little more than 8 mmm. Often two and three are seen connected together, forming moniliform chains. It is by the active growth and development of the cells during this process that the glucose of the solution is decomposed, and alcohol and carbonic acid produced in its place. Another species of saccharomyces forms the fungus of bread-yeast, and a third the ferment of grape-juice by which it is made to undergo the vinous fermentation.

When fermentation is used as a test, a little beer-yeast is added to the supposed saccharine fluid, and the mixture kept at the temperature of about 25° (77° F.). The gas which is given off during the process is collected and examined, and the remaining fluid is purified by distillation. If the gas be found to be carbonic acid, and if the distilled liquid contain alcohol, there can be no doubt that a fermentable sugar was originally present in the solution. Glucose undergoes fermentation more readily and completely than most other varieties of sugar.

Lactose, $C_{12}H_{24}O_{12}$, or *Sugar of Milk*.

This is the variety of sugar which is found in milk, the only fluid in which it is known to occur. It is less freely soluble than glucose, and its sweet taste is less marked. In watery solution it rotates the plane of polarization to the right 58°.20. In chemical composition it is isomeric with glucose, which it resembles in several of its reactions, namely, in being decomposed and turned brown by boiling alkalies, in readily reducing the copper-oxide in Trommer's and Fehling's tests, and in undergoing the alcoholic fermentation under the influence of yeast. It enters into fermentation, however, very slowly, as compared with glucose, and the process is usually incomplete. If fermentation go on in the milk itself, or in the presence of other ingredients of the milk, a part of the sugar is converted into lactic acid, $C_3H_6O_3$, also a carbo-hydrate. By boiling for some time with dilute sulphuric or hydrochloric acid, lactose becomes readily and completely fermentable. This sugar forms an important element in the food of the young infant, being a constant ingredient of the milk. It is not known from what substance it is formed in the tissues of the mammary gland;

but it is evidently a reserve material, intended for the nutrition of the infant, and not for consumption in the body of the parent.

Saccharose, $C_{12}H_{22}O_{11}$, or *Cane Sugar.*

This variety, the oldest known species of sugar, is derived from the juices of the sugar cane, where it exists in great abundance. It solidifies on cooling from a hot concentrated solution in the well-known white granular crystalline masses, the form in which it is generally used for culinary purposes. If crystallized more slowly, it furnishes large, colorless, prismatic crystals, in which form it is known as "rock candy" or "sugar candy." This sugar is also manufactured from the juices of the beet-root, and, imperfectly purified, from those of the sorghum and the sugar-maple. It exists to some extent in the green stems of Indian corn, in sweet potatoes, in parsnips, turnips, and carrots, and in the spring juices of the birch and walnut trees. Honey is a mixture of glucose and saccharose, together with various other substances.

Cane sugar originates from glucose, in the process of vegetation, by a change the reverse of that by which glucose itself is formed from starch, that is, by the loss of oxygen and hydrogen in the proportions to form water. A comparison of the chemical composition of the two substances will show the manner in which the transformation takes place, namely :—

$$\underset{\text{Glucose.}}{2(C_6H_{12}O_6)} - \underset{\text{Water.}}{H_2O} = \underset{\text{Cane sugar.}}{C_{12}H_{22}O_{11}}.$$

Saccharose is the most soluble of all the sugars, and has the strongest sweet taste. It rotates the plane of polarization to the right 73°.84. It differs in its reactions from glucose by the fact that it is not turned brown by boiling with an alkali, and does not reduce the copper-oxide in Trommer's test, or does so very slowly and imperfectly. It may be converted into glucose, however, by a few seconds' boiling with a trace of dilute mineral acid, and will then react promptly both with boiling alkalies and with Trommer's test. Cane sugar is not immediately fermentable, but by contact with yeast it is after a time changed into glucose, and finally enters into fermentation. As it occurs in the tissues of the living vegetable, it is regarded as a reserve material, which is subsequently reconverted into glucose for the purposes of nutrition.[1] When taken as food, it is transformed into glucose by the intestinal fluids in the digestive process.

Sugar and starch, accordingly, in all their varieties, are closely allied to each other, both in their chemical and physiological relations. Their proportions of hydrogen and oxygen are such as to have given them, as a class, a distinct name, and their mutual convertibility in the process of vegetation has been shown by abundant investigations. Starch and sugar, in the living plant, represent the same nutritive material under

[1] Mayer, Agrikultur-Chemie, Band i. p. 122.

two different conditions; starch being the substance in the form of a solid deposit, and glucose in the form of solution and activity.[1] In the animal body, the glycogen of the liver is converted into soluble glucose, and thus enters the circulation before it takes an active part in the nutritive operations; and vegetable starch, when taken as food, undergoes the same transformation in the intestinal canal. Finally these substances, from whatever source they may be derived, are completely decomposed in the interior of the system, and do not reappear, in any notable quantity, in the excreted fluids of the body.

IV. Fats.

The fatty matters, or fixed oils, are distinguished from the preceding group, so far as regards their chemical composition, by the fact that they do not contain hydrogen and oxygen in the proportions to form water, the oxygen being present in smaller quantity; and also by their large proportion of carbon, which preponderates much, by weight, over the other two elements. This fact is probably connected with the strongly marked inflammability which constitutes one of their most useful properties, the oils being decomposed at a temperature of 300° (570° F.), and burning with a bright flame. The peculiarly smooth consistency of the oleaginous matters is also one of their distinguishing features, and enables them to be employed as lubricating substances, to diminish the friction between opposite surfaces.

The fats are all insoluble in water, slightly soluble in alcohol, and freely soluble in ether, which is accordingly used with advantage in extracting them from their admixture with other organic matters. They are also readily soluble in each other. They exhibit no rotatory action upon polarized light. They are all fluid at a high temperature, and crystallize on being cooled down to the requisite point; the precise degree at which crystallization takes place varying for the different kinds of fats.

The fats are not only insoluble in water, but they refuse to mix with it, even after prolonged mechanical agitation; and as soon as the two fluids are left at rest they separate from each other, the water remaining below, and the oil rising to the surface, where it collects as a distinct layer. But if the watery fluid contain a trace of free alkali, the oil is broken up into minute particles, which are disseminated uniformly throughout the fluid and held in permanent suspension. Such a fluid is called an *emulsion*, and presents an opaque white color, owing to the intimate mixture of watery and oleaginous particles having different refractive powers. In an emulsion, the oil does not suffer any chemical modification, but is simply broken up into a state of minute dissemination. It can be recovered, with all its original characters, by evaporating the watery fluid and extracting the oil from the dry residue by means of ether. Oil may also be emulsioned by contact

[1] Sachs, Traité de Botanique. Paris, 1874, p. 840.

with certain nitrogenous organic matters of an albuminous nature. White of egg, or the serum of blood, exerts this effect in an energetic manner, and the fatty substances of milk are held in suspension by its liquid albuminous ingredients.

Another characteristic of the true fatty substances is their property of *saponification*, that is, of forming soaps when subjected to certain chemical influences. If either of the natural fats be boiled for a considerable time in the watery solution of a free alkali, it is decomposed, with the production of two new bodies—first, glycerine ($C_3H_8O_3$), a neutral fluid substance which is soluble in water; and secondly, a fatty acid which combines with the alkali and forms a soap. An analogous change is thought to take place with a portion of the fatty matters in the animal fluids.

The fats are derived from both the animal and the vegetable world. They are present in many of the solids and fluids of the living body, and are found also in many varieties of vegetable food. The following list gives the proportion of fat in various alimentary substances, according to the tables of Payen:—

Quantity of Fat in 100 Parts in

Wheat	2.10	Beef's flesh (average)	5.19
Indian corn	8.80	Calf's liver	5.58
Potatoes	0.11	Mackerel	6.76
Beans	2.50	Salmon	4.85
Peas	2.10	Oysters	1.51
Sweet almonds	24.28	Cow's milk	3.70
Chocolate nut	49.00	Fowl's egg	7.00

Beside entering as an ingredient into the above articles, fat is often taken with the food in a pure, or nearly pure form, as butter, olive oil, or the various kinds of adipose tissue.

Fat is produced in the vegetable tissues, perhaps to some extent directly from carbonic acid and water, but certainly in considerable quantity by transformation of the starch originally formed.[1] It is from this source that the fat so abundantly stored up in oily seeds and fruits is mainly derived; and in this situation it is retained until required for the purposes of germination and growth. It is accumulated in some seeds and fruits in remarkable quantity, particularly in those of the sweet and bitter almond, the chocolate tree, hemp, flax, ricinus communis, and Croton tiglium, where it exists in the proportions of from 24 to 60 per cent.

The three most important varieties of fat are those known as *Stearine*, *Palmitine*, and *Oleine*. They resemble each other in their general characters, and differ mainly in their degree of fluidity at corresponding temperatures; stearine solidifying the most readily of the three, while oleine remains fluid at a lower temperature than either of the others.

[1] Mayer, Agrikultur-Chemie, Band i. pp. 84, 85.

Stearine, $C_{57}H_{110}O_6$,

So called from the readiness with which it assumes the solid form, is a main ingredient of the more consistent fats. It liquefies, when pure, at about 60° (140° F.), and again solidifies when the temperature falls to or a little below this point. It crystallizes, on cooling from a warm solution in oleine, in fine radiating needles which often follow a wavy or curvilinear direction. It is rather less freely soluble in alcohol and ether than the other fatty substances.

Fig. 8.

STEARINE, crystallized from a warm solution in Oleine.

Palmitine, $C_{51}H_{98}O_6$,

Was first recognized as an ingredient of *palm oil*, a semi-solid fat obtained from the seed of an African palm. It crystallizes, on cooling from its concentrated alcoholic or ethereal solution, in the form of slender needles. It liquefies about the temperature of 46° (115° F.). It is found in considerable abundance in a variety of animal and vegetable fats.

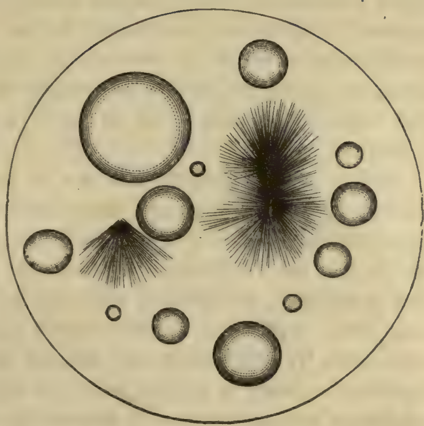
Oleine, $C_{57}H_{104}O_6$.

As its name indicates, this is the representative ingredient of the *oils*, or liquid fatty substances. When pure it is transparent and colorless. It retains its fluidity at all ordinary temperatures, and even below the freezing point of water. It readily dissolves both stearine and palmitine, its solvent power for these substances increasing with the elevation of the temperature.

None of these oleaginous substances occur naturally in an isolated form, but they are mingled together in varying proportions in all the ordinary animal and vegetable fats and oils. The consistency of the mixtures varies with the relative quantity of their different fatty ingredients. Thus the more solid fats, such as suet and tallow, consist largely of stearine; the softer fats, as lard, butter, and the ingredients of human adipose tissue, contain a greater abundance of palmitine; while the liquid fats, like the fish oils, olive oil, and nut oil, are composed mainly of oleine. As a general rule, in the bodies of the warm-blooded animals these mixtures are fluid, or very nearly so, in consistency; for, although both stearine and palmitine, when pure, are solid at the ordinary temperature of the body, they are held in solution during life by the oleine with which they are associated. After

death, as the body cools, the stearine and palmitine sometimes separate in a crystalline form, since the oleine can no longer hold in solution so large a quantity as it had dissolved at a higher temperature. (Fig. 9.)

Fig. 9.



OLEAGINOUS PRINCIPLES OF HUMAN FAT. Stearine and Palmitine crystallized; Oleine fluid.

When in a fluid state, the fatty substances present themselves in the form of drops or globules, which vary greatly in size, but which may be readily recognized by their optical properties. They are circular in shape, with a sharp well-defined outline. They often have a faint amber color, which is distinctly marked in the larger globules, less so in the smaller. As they have a higher refractive power than the watery fluids in which they are immersed, they act under the microscope as double convex lenses, and concentrate the light transmitted through them, at a point above the level of the liquid. Consequently, they present the appearance of a bright centre surrounded by a dark border. If the lens of the microscope be lifted farther away, the centre of the globule becomes brighter, and its borders darker. These characters will usually be sufficient to distinguish them from other fluid globules of less refractive power.

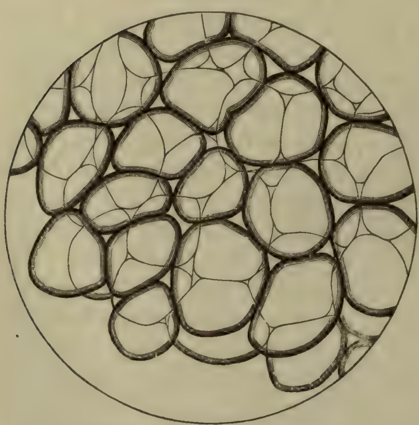
The oleaginous matters present a striking peculiarity in regard to the form under which they occur in the living body, and one which distinguishes them from other ingredients of the animal solids and fluids. The remaining proximate principles of different groups are intimately associated together by molecular union, so as to form either clear solutions or homogeneous solids. Thus the saccharine matters of the blood or the milk are in solution in water, in company with the albumen, the lime phosphate, sodium chloride, and the like; all of them equally distributed throughout the general mass of the fluid. In the bones and cartilages, the animal matters and the calcareous salts are in similarly intimate union with each other; and in every other part of the body the animal and inorganic ingredients are united in a similar way. But it is different with the fats. For, while the three principal varieties of oleaginous matter are united with each other, they are not united, as a general rule, with proximate principles of other kinds; that is, with water, saline substances, sugar, or albumen. The fats are soluble to a certain extent in the ingredients of the bile, and they are found in small quantity, in the saponified condition, in the plasma of the blood, as sodium stearate, palmitate, or oleate. But in by far the larger propor-

tion of cases, instead of forming a homogeneous solid or fluid with the other proximate principles, the oleaginous matters are found in distinct masses or globules, suspended in the serous fluids, interposed in the interstices between the anatomical elements, included in the interior of cells, or deposited in the substance of fibres or membranes. Even in the vegetable tissues, oil is always deposited in distinct drops or granules.

Owing to this fact, the oils can be easily extracted from the organized tissues by the employment of mechanical processes. The tissues, animal or vegetable, are cut into small pieces and subjected to pressure, by which the oil is forced out from the parts in which it was entangled, and separated, sometimes without further manipulation, in a state of comparative purity. A moderately elevated temperature facilitates the operation by increasing the fluidity of the oleaginous matter; but no chemical agency is required for its separation. Under the microscope, oil-drops and granules can be readily distinguished from the remaining parts of a tissue, and may also be recognized by the dissolving action of ether, which acts upon them, for the most part, without attacking the other proximate principles.

Oils are found, in the animal body, most abundantly in the adipose tissue. Here they are contained in the interior of the adipose vesicles, the cavities of which they completely fill, in a state of health. These vesicles are transparent, and have a partly angular form, owing to their mutual compression. (Fig. 10.) They vary in diameter, in the human subject, from 28 mmm. to 125 mmm., and are composed of a thin, structureless animal membrane, forming a closed sac, in the interior of which the oily matter is contained. The oil, accordingly, is simply included mechanically in the interior of the vesicles. Sometimes, when emaciation is going on, the oil partially disappears from the cavity of the adipose vesicle, and its place is taken by a watery serum; but the serous and oily fluids remain distinct, and occupy different parts of the cavity of the vesicle.

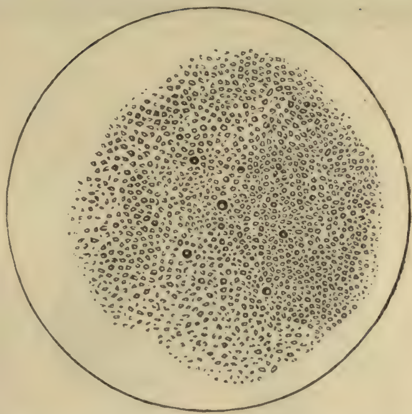
Fig. 10.



Human Adipose Tissue.

In the chyle, the oleaginous matter is in a state of *emulsion* or suspension in the form of minute particles in a serous fluid. Its subdivision is here more complete, and its molecules more minute, than anywhere else in the body. It presents the appearance of a fine granular dust, which has been known by the name of the "molecular base of the chyle." A few of these

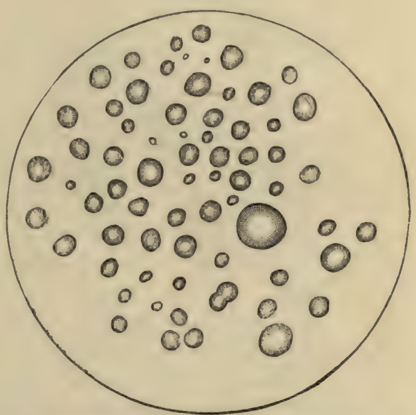
Fig. 11.



CHYLE, from commencement of Thoracic Duct, from the Dog.

granules are to be seen which measure 2.5 mmm. in diameter; but they are generally much less than this, and the greater part are so small that they cannot be accurately measured. (Fig. 11.) For the same reason they do not present the brilliant centre and dark border of the larger oil-globules; but appear by transmitted light only as minute dark granules. The white color and opacity of the chyle, as of all other fatty emulsions, depend upon this molecular condition of the oily ingredients. The albumen and salts, which are in intimate union with each other, and dissolved in the water, would alone make a colorless and transparent fluid; but the oily matters, suspended in distinct particles, with a different refractive power from that of the serous fluid, interfere with its transparency, and give to the mixture the white color and opaque appearance which are characteristic of emulsions. The oleaginous nature of these particles is readily shown by their solubility in ether.

Fig. 12.



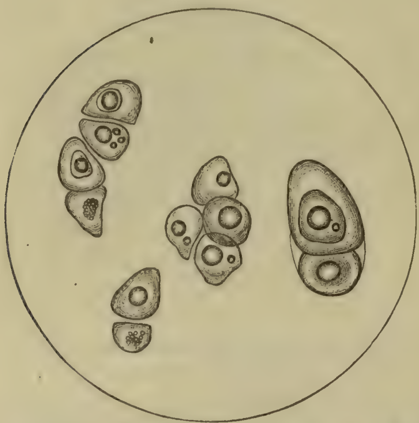
GLOBULES OF COW'S MILK.

In the milk, the oily matter occurs in larger masses than in the chyle. In cow's milk (Fig. 12), the oil-drops, or "milk-globules," are not quite fluid, but have a pasty consistency, owing to the large quantity of palmitine which they contain, in proportion to the oleine. When forcibly amalgamated with each other and collected into a mass by prolonged beating or churning, they constitute butter. In cow's milk, the globules vary somewhat in size, but their average diameter is 6 mmm. They are suspended in the serous fluid of the milk, and by heating may be more perfectly liquefied, and made to assume a circular form.

In the cells of the laryngeal, tracheal, and costal cartilages (Fig. 13) there is always more or less fat deposited in the form of rounded globules, somewhat similar to those of the milk.

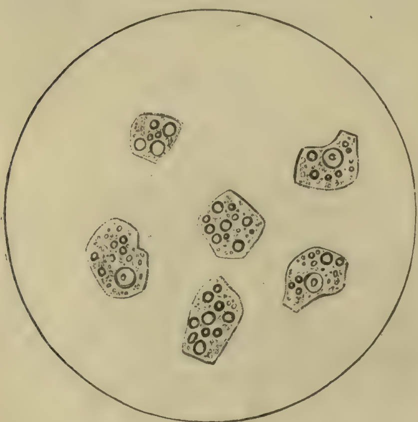
In the glandular cells of the liver, oil occurs constantly, in a state of health. It is here deposited in the substance of the cell (Fig. 14), generally in smaller globules than the preceding. In some cases of disease, it accumulates in excessive quantity, and produces the state known as fatty degeneration of the liver. This is consequently only an exaggerated condition of that which normally exists in health.

Fig. 13.



Cells of Costal Cartilages, containing oil-globules. Human.

Fig. 14.



Hepatic Cells. Human.

In the carnivorous animals oil exists in considerable quantity in the convoluted portion of the uriniferous tubules. (Fig. 15.) It is here in the form of granules and rounded drops, which sometimes appear to fill nearly the whole calibre of the tubules.

It is found also in the secreting cells of the sebaceous and other glandules, deposited in the same manner as in those of the liver, but in smaller quantity. It exists, beside, in large proportion, in a granular form, in the secretion of the sebaceous glandules.

It occurs abundantly in the marrow of the bones, both under the form of free oil-globules and inclosed in the vesicles of adipose tissue, and is found in considerable quantity in the substance of the yellow wall of the corpus luteum.

It occurs also in the form of granules and oil-drops in the muscular fibres of the uterus (Fig. 16), in which it begins to be deposited soon after delivery, and where it continues to be present during the whole period of the resorption or involution of this organ.

In all these instances, the oleaginous matters remain distinct in form and situation from the other ingredients of the tissues, and are only mechanically entangled among the fibres and cells, or imbedded in their interior.

A large part of the fat which is found in the animal body may be accounted for by that which is taken in with the food, since oily matter occurs in both animal and vegetable substances. Fat is, however, formed in the body from other organic substances, independently of what is introduced with the food. This important fact has been definitely ascertained by the experiments of MM. Dumas and Milne-Edwards on bees,[1] M. Persoz on geese,[2] and finally by those of M. Boussingault on geese, ducks, and pigs.[3] The observers first ascertained the quantity of fat existing in the whole body at the commencement of the experiment. The animals were then subjected to a definite nutritious regimen, in which the quantity of fatty matter was duly ascertained by analysis. The experiments lasted for a period varying, in different instances, from thirty-one days to eight months; after which the animals were killed and all their tissues examined. The result of these investigations showed that considerably more fat had been accumulated by the animal during the course of the experiment than could be accounted for by that which existed in the food; and placed it beyond a doubt that oleaginous substances may be, and actually are, formed in the interior of the animal body by the decomposition or metamorphosis of other proximate principles.

Fig. 15.

URINIFEROUS TUBULES OF DOG, from cortical portion of kidney.

Fig. 16.

MUSCULAR FIBRES OF HUMAN UTERUS three weeks after parturition.

There is reason to believe that fat is produced in this way, under the influence of the vital process, from the transformation of starchy and saccharine substances. In the first place, as we have already seen, there

[1] Annales de Chim. et de Phys., 3d series, vol. xiv. p. 400. [2] Ibid., p. 408.
[3] Chimie Agricole. Paris, 1854.

is no doubt that fat is produced from starch and glucose in vegetables during a certain period of their growth. The oily seeds of certain plants while still immature contain starch; but as they ripen, the starch diminishes or disappears and oil takes its place.[1]

It is also a matter of common observation that articles of food, consisting largely of starch or sugar, or of both, are especially apt to be fattening, both for man and animals and in sugar growing countries, during the short season occupied in extracting and preparing the sugar, the horses and cattle, as well as the laborers employed on the plantation, all of whom partake freely of the saccharine juices, grow remarkably fat, and again lose their superabundant flesh when the season is past. It is not known, however, whether the saccharine matters in these instances are directly converted into fat, or whether they pass through a series of intermediate changes which furnish the materials for its formation. The abundant accumulation of fat in certain regions of the body and its absence in others, and more particularly its constant occurrence in situations to which it could not have been transported by the blood, as the interior of the cells of the costal cartilages, make it probable that oily matter is often formed from the metamorphosis of other proximate principles, upon the very spot where it makes its appearance in the solid tissues. Cases of hereditary obesity, and of obesity occurring only after a definite period of life, indicate also that the excessive deposition of fat may be due to internal causes dependent on the special condition of the bodily system.

In the female during lactation, a large part of the oily matter introduced with the food, or formed in the body, is discharged with the milk, and goes to the support of the infant. But in the female in the intervals of lactation, and in the male at all times, the oily matters almost entirely disappear by decomposition in the interior of the body; since the small quantity which is discharged with the sebaceous matter by the skin bears only an insignificant proportion to that which is introduced daily with the food.

Beside the fats proper there is also contained in the body the following substance, which resembles fat in the general features of its chemical composition, and in some of its reactions, but differs from them in three important particulars, namely: 1st, in being volatile at a high temperature; 2d, in exerting a rotatory action on polarized light; and 3d, in the fact that it cannot be transformed, by the action of alkaline solutions, into glycerine and a fatty acid—that is, it is not saponifiable.

Cholesterine, $C_{26}H_{44}O$,

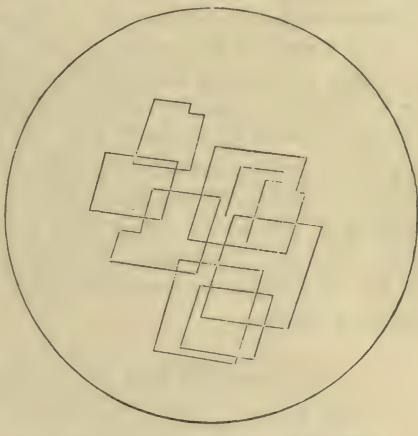
So called from its being often precipitated as a solid deposit from the bile, in which form it was first discovered. Cholesterine is an ingredient in the blood-plasma and the blood-globules, in the bile, in the sebaceous

[1] Prof. S. W. Johnson, How Crops Grow. New York, p. 94.

matter of the skin, the liver, the spleen, the crystalline lens, and especially in the nerves, spinal cord, and brain, in which last it has been found by Flint[1] in the proportion on the average of about one part per thousand. Recent observations have shown that it is also a constituent of various articles of food, such as the yolk of egg, and even of many vegetable products, as peas, beans,[2] olives, almonds, and Indian corn.[3]

Cholesterine is a crystallizable substance, insoluble in water, freely soluble in ether, chloroform, boiling alcohol, and the volatile and fatty oils. It is partially soluble in watery solutions of the biliary salts and of the saponified fats. It is deposited from its alcoholic or ethereal solution in the form of very thin, colorless, transparent, rhomboidal plates, portions of which are often cut out by lines of cleavage parallel to the edges of the crystal. They frequently occur deposited in layers, in which the outlines of the subjacent crystals show very distinctly through the substance of those placed above. It is often found, in a crystalline form, in the fluid of hydrocele and other morbid exudations, in the contents of encysted tumors, and in biliary calculi. Crystallized cholesterine melts at 145° (293° F.), and distils unchanged in vacuo at about 360° (680° F.). Its solutions rotate the plane of polarization to the left 32°.

Fig. 17.



CHOLESTERINE, from an Encysted Tumor.

If cholesterine be triturated with strong sulphuric acid, and chloroform added to the mixture, a blood-red color is produced, which afterward disappears by exposure to the air, passing gradually from red to violet, blue, and green, the solution finally becoming colorless.

Our knowledge with regard to the physiological relations of cholesterine is less definite than as to those of the true fatty substances. Its abundant proportion in the brain and nerves, and its association in these tissues with other important constituents, have led to the opinion that it is an essential ingredient of the nerve substance. Whatever may be its source in these organs, it is no doubt absorbed from the nervous system by the blood, carried to the liver, and thence discharged with

[1] American Journal of the Medical Sciences, October, 1862.

[2] Hoppe-Seyler, Handbuch der Physiologisch- und Pathologisch-Chemischen, Analyse. Berlin, 1870, p. 98.

[3] Hardy, Principes de Chimie Biologique. Paris, 1871, p. 123.

the bile. According to the observations of Prof. Flint, Jr., on the dog,[1] its quantity in the blood increases, while passing through the brain, from 0.52 to 1.09 parts per thousand. Authorities differ as to whether it is discharged with the feces, or is transformed in the interior of the body.

The most important characteristic, in a physiological point of view, of all the proximate principles of the second class, including the amylaceous, saccharine, and oily substances, relates to their source and their final destination. Not only are they of organic origin, making their appearance first in the interior of vegetables; but they are all produced also, to a certain extent, from other organic materials, in the bodies of animals; continuing to be formed when no similar substances, or only an insufficient quantity of them, have been taken with the food. Furthermore, when introduced with the food, or formed in the body and deposited in the tissues, these substances are not found in the secretions. They, therefore, for the most part, disappear by decomposition in the interior of the body. They pass through a series of changes by which their essential characters are destroyed; and they are finally replaced in the circulation by other substances, which are discharged with the excreted fluids.

[1] Physiology of Man, vol. iii. New York, 1870, pp. 281, 282

CHAPTER IV.

ALBUMINOUS MATTERS.

THE proximate principles belonging to this class are very important, not only from their peculiar physiological properties, but also from their comparatively abundant quantity in the animal body. They are derived both from animal and vegetable sources. But in plants, as a general rule, the albuminous matters, though constantly present, and essential to the activity of vegetative life, are in small quantity as compared with other ingredients of the fully developed tissues. In man and animals, on the other hand, they constitute by far the larger part of all the solid constituents of the body. Everywhere their chemical constitution, their physical characters, and the distinctive properties which belong to them, show that they have an intimate connection with the more active phenomena of living beings.

The first peculiarity by which they are distinguished from the proximate principles of the preceding class, is that they contain *nitrogen*, in addition to the three elements belonging to other organic bodies, namely, carbon, hydrogen, and oxygen. They are, therefore, sometimes called the "nitrogenous" proximate principles. But, as we shall hereafter see, there are various other substances, of a crystallizable nature, also containing nitrogen, which are produced in the body, and which are of a different character from the albuminous matters.

The albuminous matters are not crystallizable. They always, when pure, assume an amorphous condition, in which they are sometimes solid, as in the bones; sometimes fluid, as in the plasma of the blood; and sometimes semi-solid in consistency, or midway between the solid and fluid condition, as in the muscles and the substance of the glandular organs. Even in the fluids, the albuminous matters, when present in considerable quantity, as in the blood-plasma, the pancreatic juice, or the submaxillary saliva, give to the solution a peculiar viscid or mucilaginous consistency. This consistency is more marked, in proportion to the abundance of the organic ingredients. The albuminous matters, in solution, all rotate the plane of polarization toward the left. The precise chemical constitution of these substances has not been in all cases determined. The apparent variation in the exact proportion of their ultimate elements in different instances is probably due to the readiness with which they become modified in the processes of nutrition, many of them passing into each other under the influence of digestion and assimilation. There are, no doubt, a great variety of these matters existing in the body, only a certain number of

which have as yet been so distinctly recognized as to receive specific names. Many of them, perhaps all, contain a small amount of sulphur in addition to their carbon, hydrogen, oxygen, and nitrogen. Their chemical relation to other substances has not been found sufficiently definite, in any case, to establish the formula for their atomic constitution. The average proportion, however, by weight, of their constituent elements, according to the tables of Hoppe-Seyler[1] and Frémy, is as follows:—

AVERAGE COMPOSITION OF ALBUMINOUS MATTERS.

Carbon	52.0
Hydrogen	6.9
Nitrogen	15.6
Oxygen	24.0
Sulphur	1.5
	100.0

One of the simpler physical characters of the albuminous substances is that they are *hygroscopic.* As met with in different parts of the body, they present different degrees of consistency; some being nearly solid, others more or less fluid. But on being subjected to evaporation they all lose water, and may finally be reduced to the perfectly solid form. If after this desiccation they be exposed to the contact of moisture, they again absorb water, swell, and regain their original mass and consistency. This phenomenon is different from that of capillary attraction, by which some inorganic substances or tissues become moistened when exposed to the contact of water; for in the latter case the water is simply entangled mechanically in the meshes and pores of the inorganic body, while that which is absorbed by the albuminous matter is actually united with its substance, and diffused equally throughout its entire mass. Every albuminous matter is naturally united in this way with a certain quantity of water, some with more, some with less. Thus the albumen of the blood is in union with so much water that it has the fluid form, while the corresponding substance of cartilage contains less and is of a firmer consistency. The quantity of water contained in each albuminous substance may be diminished by artificial desiccation, or by a deficient supply; but it cannot be increased beyond a certain amount. Thus, if the albumen of the blood and the albuminous matter of cartilage be both reduced by evaporation to a similar degree of dryness, and then placed in water, the albumen will absorb so much as again to become fluid, but the cartilaginous substance only so much as to regain its usual nearly solid consistency. Even where the organic substance, therefore, as in the case of albumen, becomes fluid under these circumstances, it is not precisely by its solution in water, but only by its reabsorption of that quantity of fluid with which it was naturally associated.

[1] Handbuch der Physiologisch- und Pathologisch-Chemischen Analyse. Berlin, 1870.

Another characteristic feature of the proximate principles of this group is their property of *coagulation.* Those which are naturally fluid suddenly assume, under certain conditions, a solid or semi-solid consistency. They are then said to be coagulated; and, when once coagulated, they cannot usually be made to resume their original condition. This property of coagulability is not only a marked quality of the albuminous matters as a class, but it often serves to distinguish them from each other by the different special conditions under which it is manifested by each one. Thus the substance producing fibrine coagulates spontaneously on being withdrawn from the bloodvessels; albumen, on being subjected to the temperature of boiling water; caseine, on being placed in contact with an acid. When an albuminous substance thus coagulates, the change which takes place is a peculiar one, and differs from that by which a mineral salt is precipitated from its watery solution. The albuminous matter, in coagulating, appears to assume a special condition, and to permanently change its properties; but, in passing into the solid form, it still retains all the water with which it was previously united. Albumen, when coagulated, retains the same quantity of water in union with it which it held before. After coagulation, this water may be driven off by evaporation, in the same manner as previously; and on being once more exposed to moisture, the organic matter will again absorb the same quantity, though it will not assume the liquid form. The coagulated substance may sometimes be dissolved by certain chemical agents, as the caustic alkalies; but it is not by this means restored to its original condition. It rather suffers a still further alteration.

In many instances we are obliged to resort to coagulation in order to separate an albuminous substance from the other proximate principles with which it is associated. This is the case, for example, with the fibrine of the blood, which is obtained in the form of flocculi, by beating freshly-drawn blood with a bundle of rods. But when separated in this way, it is already in an unnatural condition, and no longer represents exactly the original fluid fibrine as it existed in the circulating blood. Nevertheless, this is the only mode in which it can be examined, as there are no means of bringing it back to its previous condition.

Another important property of the albuminous matters is that they excite, in other proximate principles and in each other, those peculiar indirect chemical changes which have been termed *catalyses* or *catalytic transformations.* That is to say, they produce the changes referred to, not directly, by combining with the substance which suffers alteration, or with any of its ingredients; but simply by their presence, which induces the chemical change in an indirect manner. We do not understand the manner in which these changes are accomplished, but the influence thus exerted by the albuminous matters is a very marked one, and is of great importance in many of the acts of animal and vegetable nutrition. A comparatively small quantity of the catalytic body is often capable of inducing a palpable change in a large quantity of

another substance. The action of vegetable diastase in converting starch into dextrine and glucose is a process of this nature; and it is found that one part of diastase is capable of effecting the transformation of 2000 parts of starch. The albuminous ingredients of the saliva, of the pancreatic and intestinal juices, exert a similar action on hydrated starch. The whole process of digestion and assimilation is in great part made up of a series of such catalytic changes, in which the nutritious matters undergo their requisite transformations, by contact with special albuminous ingredients of the blood, the tissues, or the secretions.

At a temperature of 300° (570° F.) or over, the albuminous matters, like other organic substances, are destroyed and decomposed into gaseous products. But if subjected for a certain time to a temperature of about 125° (257° F.), they undergo a change in addition to their coagulation, by which a distinct and agreeable flavor is developed, and by which they become suitable for use as human food. It is this change which is produced in the process of *cooking*, and the peculiar flavor which results always depends upon the presence of a certain quantity of albuminous matter in the substance employed. If the temperature at which the cooking process is carried on be too low, the characteristic flavors are not developed; if it be too high, they are destroyed and replaced by empyreumatic odors, from the combustion or decomposition of the ingredients of the food.

Lastly, the albuminous matters are distinguished by the property of *putrefaction*. This is a process by which dead animal substances, when exposed to the atmosphere at a moderately warm temperature, gradually soften and liquefy and are finally decomposed, with the production of certain fetid and unwholesome gases, among which are hydrogen sulphide and carbide, usually with more or less carbonic acid, nitrogen, and ammoniacal vapors. The mixture of these emanations causes an odor which is easily recognized as a "putrefactive odor;" and wherever such emanations are perceived, it is an indication that some substance containing albuminous matters is undergoing decomposition. As these albuminous matters are more abundant in the tissues and fluids of animals than in those of vegetables, the phenomena of putrefaction are also most distinctly marked in the decay of animal substances. But they will take place in both, under the requisite conditions. A solution of nitrogenous vegetable matters will present all the essential characters of putrefaction, though not developed with the same degree of intensity as in fluids of animal origin.

In order that putrefaction may take place certain special conditions are necessary. In the first place it requires the access of atmospheric air, or of some fluid containing oxygen. If the putrescible substance be first boiled so as to expel all the free oxygen contained in its fluids, and if then, while the boiling is going on, it be inclosed in a hermetically sealed vessel, no putrefaction takes place, but the substance remains unaltered for an indefinite time. It is by this means that cooked meats

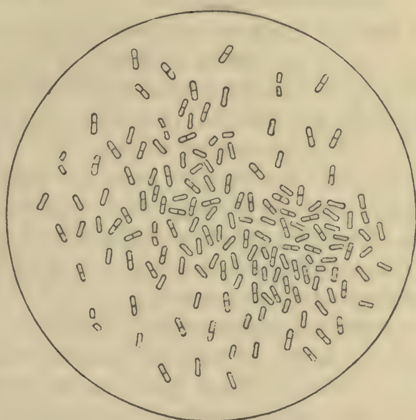
are preserved in sealed cans, for use upon long voyages or expeditions at a distance from the usual base of supplies. So long as the cans are kept perfectly closed, their contents remain sound. After they are opened and the air admitted to their interior, the food must be used at once, otherwise it will begin to putrefy after the usual interval of time.

Another essential condition for putrefaction is the presence of moisture. Albuminous substances which are reduced to a perfectly dry state do not undergo decomposition; and in some regions, where a high temperature and a dry atmosphere favor the rapid desiccation of organic substances, this fact is also utilized for the preservation of meats. Immediately after the animal is killed, the flesh is cut into thin strips and hung up to dry in the air, and, desiccation being completed before putrefaction has commenced, the food thus prepared is preserved for an indefinite time.

The third requisite for putrefaction is a moderately elevated temperature. It goes on most rapidly between 25° and 35° (77° to 95° F.). Below 25° it gradually diminishes in activity, and ceases altogether about the freezing point of water. Meats, therefore, which are kept frozen or closely packed in ice do not putrefy. The process is also suspended in all albuminous matters exposed to winter weather at the freezing point. The carcass of an extinct mammoth has even been found imbedded in ice in Northern Siberia, which was in such a state of preservation that its flesh was used for food by dogs and other animals.[1] A temperature much above 35° is also unfavorable to the putrefactive change, and it is completely arrested by a heat approaching that of boiling water.

The process of putrefaction is accomplished by the growth and multiplication of a microscopic vegetable organism, somewhat analogous to that by which fermentation is excited in saccharine fluids. If any clear solution containing animal or vegetable albuminous matters be exposed to the air at a moderate temperature, after a short time it becomes turbid. This turbidity is due to the development of minute vegetable cells, of very simple organization, which multiply with great rapidity in

Fig. 18.



CELLS OF BACTERIUM TERMO; from a putrefying infusion.

[1] Mémoires de l'Académie Impériale des Sciences de St. Petersbourg, tome 5, p. 440.

the decomposing liquid, and produce in it, by their vegetative activity, the changes of putrefaction. These cells belong to the genus "Bacterium," so called from their simple rod-like form; and the species which is invariably to be found in putrefying infusions is known by the name of *Bacterium termo*. The cells are of an oblong form, and average 3 mmm. in length by 0.6 mmm. in thickness. They are usually double, consisting of two single cells placed end to end. While actively growing in a putrefying infusion, they are in constant process of multiplication, by which their numbers are rapidly increased. The multiplication takes place by spontaneous division of the cell, by a transverse partition which grows across its middle. After a time the two cells, thus formed out of a single one, separate from each other, and each repeats the process for itself.

One of the most remarkable characters of the bacterium cells is their active spontaneous movement. During a certain period of their development they are in incessant and rapid motion by means of a conical rotation about their longitudinal axis, by which they are transported in various directions through the fluid in which they are contained. This motion is often so rapid that it can hardly be followed by the eye; in other instances it is so slow that its mechanism may be distinguished by careful examination. The movement and mutiplication of the bacterium cells go on while putrefaction continues. After all the albuminous ingredients of the infusion have been decomposed, the liquid again becomes clear, and the bacterium cells subside to the bottom in a quiescent whitish layer. A small portion of this layer will readily excite putrefaction, if added to another albuminous liquid.

As the bacterium cells effect the decomposition of albuminous matters by their own vegetative activity, it is for this reason that putrefaction is limited by certain special conditions, already mentioned. Bacteria belong to the group of colorless cryptogamic vegetables. Like other plants of this kind, they assimilate directly organic substances ready formed, and at the same time absorb oxygen and exhale carbonic acid, after the manner of animals. Consequently oxygen is one of the substances essential to their growth; and, as putrefaction takes place only by means of their vital activity, oxygen or atmospheric air must be present in order to allow putrefaction to go on. Furthermore the presence of moisture is necessary to their growth, as it is to that of all other plants; and a substance thoroughly dried cannot putrefy, since no vegetative development is possible in the total absence of moisture. A certain degree of warmth is also essential to the continued growth of these bodies. Their development is suspended by a freezing temperature, and their vitality is destroyed by prolonged contact with boiling water.

Lastly, a certain amount of albuminous matter is necessary for the nutrition of bacteria. Their cells may remain indefinitely, in a quiescent condition, suspended in other fluids or even in pure water; but for their active development and multiplication they require the pre-

sence of albuminous matters, which appear to supply the necessary material for their growth. They decompose these substances therefore by assimilating their ingredients in the process of vegetable nutrition, and the putrefactive gases are the final result of the changes thus taking place, just as alcohol and carbonic acid are produced in the fermentation of saccharine liquids.

Fermentation and putrefaction, accordingly, are analogous processes, in which certain materials are decomposed under the influence of microscopic vegetation. The former takes place in saccharine fluids, the latter in those containing albuminous matter; since the yeast-plant requires for its growth a preponderance of non-nitrogenized hydrocarbonaceous matter, while bacterium cells are nourished mainly by the absorption of nitrogenous substances.

The following table shows the proportion of albuminous matter, according to Payen, in different substances used as food:—

Quantity of Albuminous Matter in 100 parts in

Beef flesh	19.50	Wheat grains	18.03
Fowl's eggs	12.35	Rye	12.50
Mackerel	24.31	Oats	14.39
Salmon	13.58	Indian corn	12.50
Oysters	14.01	Rice	7.55
Beans (dry)	24.40	Potatoes	2.50
Peas "	23.80	Sweet potatoes	1.50

The first formation of albuminous matter takes place in vegetables, subsequent to the production of the non-nitrogenous organic substances, starch and glucose, by the union of these last with nitrogen derived from the inorganic salts. Green plants, which have the power of generating the carbohydrates from carbonic acid and water, if supplied with moisture containing nitrates or ammonium salts in solution, are known to grow vigorously and increase many fold their contents of albuminous matter.[1] These salts must therefore have supplied the nitrogen requisite for the formation of the nitrogenous substances. The sulphur, which also enters into the composition of these substances, is derived by the plants from a reduction of the soluble sulphates contained in the soil.

Notwithstanding the very marked and important peculiarities which distinguish the albuminous matters as a group, there are many of these substances which differ from each other by a variety of secondary characters. It is possible that some of those now designated by specific names may really be mixtures of two or more distinct substances; but the classification at present in use expresses the distinguishing marks of the more important varieties, so far as they are yet known.

Fibrine.

Fibrine is found in the plasma of the blood, where it exists in the proportion, on the average, of three parts per thousand. It is also

[1] Mayer, Lehrbuch der Agrikultur-Chemie, Band i. pp. 145, 150.

present in small quantity in the lymph and in the chyle. It is this substance which is distinguished by its property of "spontaneous coagulation;" that is, it coagulates on being withdrawn from the vascular system, without the addition of any physical or chemical reagent. It is the coagulating element of the blood; and the power of freshly drawn blood to form a clot depends upon its presence as an ingredient of the circulating fluid. The term fibrine properly represents, not the solid clot obtained by coagulation, but the fluid substance existing beforehand in the blood, and which becomes solidified after its withdrawal. It is regarded by some as generated by the union of two pre-existing substances; by others, as produced from the decomposition of one. As we have, however, but little opportunity of studying it while still forming a part of the fluid plasma, our knowledge is mainly confined to its properties in the solidified form. It is obtained by stirring the freshly drawn blood with glass rods or a bundle of twigs, and afterward washing the deposited clots with distilled water until the adherent coloring matter is removed.

Coagulated fibrine is a colorless, tolerably firm, extensible, and elastic substance, which has, under the microscope, a finely fibrillated texture. It is insoluble in water, but in solutions of the caustic alkalies or the alkaline carbonates it becomes gelatinous, and is after a time, by the aid of warmth, partially dissolved. Some of the free acids, as hydrochloric, acetic, lactic, or phosphoric acid, have a similar effect. If it be heated in water or in a neutral liquid to 72° (162° F.), it becomes contracted, white, and opaque, and less extensible than before.

An albuminous matter very similar in its physical properties to animal fibrine, exists in certain vegetable substances, especially in wheat flour, where it is known as *gluten*. When freed from the admixture of other ingredients, it is tenacious, extensible, elastic, insoluble in water, and slowly soluble in dilute alkalies. Its property of tenacity and its nitrogenous character make it an important constituent of wheat flour in the manufacture of bread.

Albumen.

Albumen is found abundantly in the plasma of the blood, also in the lymph, the pericardial and cephalo-rachidian fluids, and in very small quantity in the saliva and in the milk. It is not spontaneously coagulable, but coagulates promptly when heated in its liquid form to a temperature of 72° (162° F.), and its coagulum is again soluble in the caustic alkalies. It is also coagulated by contact with nitric or sulphuric acid, alcohol, or the metallic salts. The organic acids, as acetic, lactic, or tartaric acid, do not affect it; but if it be first slightly acidulated by dilute acetic acid, it may be precipitated by a solution of potassium ferrocyanide. This is one of the most delicate tests for the presence of albumen, but it is usually recognized from its coagulability by heat and nitric acid. When dissolved in a fluid of neutral reaction, it rotates the plane of polarization to the left 56°.

The white of the fowl's egg is mainly composed of a substance also called albumen, and which corresponds with the albumen of blood in its coagulability by heat, nitric acid, alcohol, and the metallic salts. It is distinguished from the preceding mainly by its coagulability by ether, which has no effect on the albumen of blood. It rotates the plane of polarization to the left 35°.5.

The fresh juices of nearly all vegetables, and especially the succulent plants, contain a substance coagulable by heat, which has been called *vegetable albumen.* It may also be obtained from the cereal grains by extraction with water, and resembles in its principal chemical reactions the albumen derived from animal sources.

Albuminose.

This substance is closely related to albumen by its chemical composition and its general characters. It is not coagulated, however, by either heat, nitric acid, or acidulated potassium ferrocyanide, but only by the metallic salts and alcohol in excess. It is also distinguished by its ready diffusibility through animal membranes or parchment paper; while albumen, and all other liquid albuminous matters, pass through these membranes either not at all or only with great difficulty. Coagulated albumen and all other digestible albuminous matters are converted into albuminose by the action of gastric juice. They thus become liquefied and incapable of coagulation by heat. Owing to the origin of these products from the digestive act they are designated by several writers under the name of *peptones;* and a variety of them are enumerated, but their distinctive characters are not very sharply defined. Albuminose is found in the fluids of the stomach and small intestine during digestion, and exists also in the blood in the proportion of two to three parts per thousand.

Albuminose in solution has the property of modifying certain well-known chemical reactions. It interferes especially with the reduction of the copper oxide in Trommer's test. If a small quantity of glucose be dissolved in gastric juice containing albuminose, and Trommer's test applied, no peculiarity is observed on first dropping in the copper sulphate; but on the addition of potassium hydrate, the mixture takes a rich purple hue, instead of the clear blue tinge which is presented under ordinary circumstances. On boiling, the color changes to claret, cherry red, and finally to a light yellow; but no copper oxide is deposited, and the fluid remains clear. If albuminose be present only in small quantity, an incomplete reduction of the copper takes place, so that the mixture becomes opaline and cloudy, but still without any well marked deposit. This interference will take place when sugar is present in very large proportion. We have found that gastric juice, drawn from the dog's stomach during digestion, may sometimes be mixed with an equal volume of honey without giving any deposit of copper on the application of Trommer's test. If such a mixture, however, be previously diluted with water, it will often fail to prevent the

reduction and deposit of the copper oxide. The peculiar action above described depends upon the presence of albuminose, and not upon that of any original ingredient of the gastric juice; since it is not exhibited by the perfectly clear and colorless juice, obtained from the empty stomach of the fasting animal by irritation of the mucous membrane with a glass rod or metallic catheter; while the same fluid, if macerated for a time with finely chopped meat at a temperature of 38° (100° F.), will be found to have acquired the property in a marked degree. Gastric juice, furthermore, drawn from the stomach after digestion has been going on for half an hour or more, always contains a certain quantity of albuminose, and consequently interferes, as above described, with Trommer's test.

Albuminose, if present in notable quantity, will also interfere with the mutual reaction of starch and iodine. If gastric juice, containing albuminose, be mingled with an equal volume of iodine water, and a solution of starch be subsequently added, no blue color is produced; though if the iodine water be added in excess, or if the tincture of iodine be used instead of its aqueous solution, the superabundant iodine then combines with the starch, and produces the ordinary blue color. This property, like that described above, is not possessed by pure, colorless gastric juice, taken from the empty stomach, but is acquired by it on being digested with albuminoid substances.

Accordingly, in testing for the presence of glucose in fluids which are liable to contain albuminose or other organic substances of similar character, the precaution must always be adopted of first eliminating the albuminous matters which might interfere with the test. This may be done in either of two ways: first, by evaporating the fluid to dryness over the water bath, and extracting the dry residue with alcohol, which takes up the sugar, but leaves behind the albuminous matters. The alcoholic solution may then be filtered and evaporated, and the evaporated residue dissolved in water, when it will respond to Trommer's test if glucose be present. Or, secondly, the fluid may be treated with animal charcoal, which retains the albuminous matters, and allows the glucose to pass through in watery solution.

Caseine.

This is the principal albuminous ingredient of milk, the only animal fluid in which it is certainly known to exist. It is called caseine, because, when solidified, it forms the substance of cheese. It is not affected by a boiling temperature, but coagulates on the addition of any of the dilute acids, organic as well as mineral, and of magnesium sulphate. These characters are sufficient to distinguish it from albumen. It is also coagulated by a temperature of 30° (86° F.), by contact with gastric juice, or an infusion of *rennet*, the mucous membrane of the fourth stomach of the calf. In solution in neutral fluids it rotates the plane of polarization to the left 80°. Caseine is an important article of food, being the principal nutritious ingredient in preparations of milk.

A nitrogenous substance, termed *vegetable caseine*, exists abundantly in peas and beans, where it is known as "legumine." It is found also in small quantity in oats, in the potato, and in the juices of many plants. It resembles the caseine of milk in not being affected by a boiling temperature, and in its coagulability by the organic acids and magnesium sulphate.

Ptyaline

Is an ingredient of the saliva, to which it communicates the property of converting hydrated starch into glucose. From this circumstance it has sometimes been called "animal diastase." It differs from albumen in many of its characters, and is not coagulated by nitric acid nor by potassium ferrocyanide in an acidulated solution. On the other hand, it is precipitated by alcohol in excess, and by a boiling temperature; but while, after precipitation by alcohol, it may be redissolved in water with all its original properties, the action of heat produces in it a permanent alteration, and saliva which has once been boiled and allowed to cool is found to have lost its power of converting starch. Ptyaline can also be thrown down by adding to the saliva dilute phosphoric acid, and afterward neutralizing the solution with lime water. The precipitate of lime phosphate thus produced brings down with it the ptyaline, which may afterward be redissolved in water, and again separately precipitated by alcohol. Ptyaline does not constitute the whole of the organic ingredients of the saliva, but is mingled in the secretion with other albuminous substances.

Pepsine

Is the albuminous matter of the gastric juice, where it is found in the proportion of fifteen parts per thousand. It is this substance which effects the conversion of nitrogenous matters into albuminose in the digestive process. It requires, however, in order to exert this action, to be dissolved in an acidulated liquid. It also causes the coagulation of caseine, when first brought in contact with that substance. It is coagulated by a boiling temperature, and when once subjected to the action of heat loses permanently its digestive power. It is also thrown down by alcohol in excess, but may be redissolved in water after removal of the alcohol. Pepsine is produced in the glandular follicles of the stomach, and there mingled with the other ingredients of the gastric juice.

Pancreatine.

This is the characteristic ingredient of the pancreatic juice, where it is very abundant; being present in the proportion of a little over ninety parts per thousand. It is coagulable by heat, nitric acid, alcohol, and the metallic salts; in these respects resembling albumen. But it is also coagulated by magnesium sulphate, which has no effect on albumen. It is further distinguished by the fact that, after precipitation by alcohol, it may be again dissolved in water, and its solution exhibits the same

albuminous consistency which belongs to fresh pancreatic juice. It has the power of emulsifying fatty matters with great rapidity at the temperature of the living body, and also of saponifying a certain portion of them by the production of a fatty acid. It is believed by some observers that the pancreatine of pancreatic juice is a mixture of several substances; one of which, like ptyaline, is active in the conversion of starch, while another aids in the liquefaction of albuminous matters, and a third has the property of acting upon fats.

Mucosine.

There are a variety of secretions in the body which are designated by the common name of "mucus," and which are distinguished by a peculiar physical character of viscidity. This viscid consistency is given to them by the presence of a substance termed "mucosine," or, as it is called by some writers, "mucine." It exists in all the varieties of mucus, some of which, like those of the bronchial tubes and intestine, are nearly fluid, while others, like that of the cervix uteri during pregnancy, are gelatinous and semi-solid. It is also present in abundant proportion in the synovia, the bile, and the saliva of the submaxillary and sublingual glands. The secretion of the mucous follicles of the mouth consists almost entirely of it. Mucosine is not coagulated by heat, but is thrown down by alcohol and by the acids, both mineral and organic. It is remarkably unaffected by the metallic salts, lead subacetate being the only one that produces a distinct coagulation. In some cases, as in the bile, it is dissolved in the fluid ingredients of the secretion, from which it may be separated by the action of alcohol. In others, as in the urine, it is only mechanically suspended, and subsides as a light deposit after a few hours' repose.

Myosine.

The contractile substance of the striped muscular fibres contains an albuminous matter which after death coagulates, like the fibrine of the blood-plasma; at the same time the muscles lose their contractility and assume the condition of cadaveric rigidity. The coagulation of this substance is retarded by the action of cold; and it has been extracted by Kühne, from the muscular tissue of frogs, by the following process: The vascular system is first deprived of blood by an injection of a $\frac{1}{2}$ per cent. solution of sodium chloride. The muscles, thoroughly washed, are then subjected for two hours to a temperature of 7° to 10° below 0° (17° F.), reduced to a pulp in a cold mortar, and then allowed gradually to thaw upon a filter. The filtered liquid coagulates spontaneously at ordinary temperatures.

Coagulated myosine is gelatinous, and without fibrillated texture. It is insoluble in water and in concentrated solutions of common salt; but is dissolved by a watery solution of salt, made in the proportion of ten per cent. or less. It is extracted from the muscles after death by bruising the muscular tissue to a pulp in a ten per cent. solution of

sodium chloride, filtering the expressed liquid, and then precipitating the dissolved myosine by dropping the clear solution into distilled water. It may also be precipitated by adding sodium chloride in substance, and thus increasing the strength of the solution. Myosine is distinguished from the fibrine of the blood by its complete solubility in saline solutions of a certain strength, as well as in dilute acids and alkalies. When dissolved in a neutral saline fluid it is coagulable by heat, like the albumen of blood.

The preceding substances are all naturally liquid, or nearly so, in consistency, and form constituent parts of the various animal fluids and juices. The following are ingredients of the solid tissues.

Collagen.

This substance is very widely diffused in the animal body, forming the more or less homogeneous interstitial mass of the bones, periosteum, tendons, ligaments, fasciæ, and connective tissues generally. All these tissues, although at first insoluble, after long ebullition dissolve in the boiling water; and the substance thus dissolved solidifies on cooling into a jelly-like mass. This substance is *gelatine*, or the animal principle of glue. Gelatine, however, does not exist as such in the osseous and fibrous tissues in their natural condition, but is evidently the result of a transformation produced by long boiling. The original body of which these tissues are mainly composed is termed "collagen;" that is, a substance which produces gelatine or glue. The conversion of collagen into gelatine is a simple transformation, and neither a decomposition nor combination, since it is not accompanied by any increase or diminution of weight.

The gelatine produced by the action of boiling water on collagen, when present in the proportion of ten parts per thousand, solidifies on cooling; below this proportion, or if the boiling be repeated, it may remain liquid. Its solution rotates the plane of polarization to the left 130°. It is precipitated by alcohol and by tannic acid. The last, which is the only acid by which this substance is precipitated, is a very sensitive test of its presence; and, according to Hardy,[1] will detect one part of gelatine in 5000 parts of water. A similar combination no doubt takes place, in the process of tanning, between tannic acid and the original collagen of the fibrous tissues, by which they are rendered harder, more impermeable to water, and incapable of putrefaction. Gelatine is not affected by potassium ferrocyanide with acetic acid, nor by lead subacetate.

Chondrine.

The amorphous intercellular substance of cartilage resembles that of the bones and the fibrous tissues in being changed by prolonged boiling with water into a substance which will gelatinize on cooling. In

[1] Chimie Biologique. Paris, 1871, p. 282.

the case of the cartilages, however, this substance is termed *chondrine*, from the source from which it is derived. Chondrine corresponds with gelatine in most of its characters, but differs from it in being precipitated from its watery solution by both acetic acid and lead subacetate. It rotates the plane of polarization to the left 213°.5.

Elasticine.

The fibres of all the *yellow elastic tissues*, as that in the middle coat of the larger arteries, the elastic ligaments of the spinal column, and the ligamentum nuchæ, mainly consist of a homogeneous substance which possesses all the physical properties of the fibre itself, and is furthermore distinguished by its extremely refractory nature toward most chemical reagents. It is obtained by boiling the elastic fibres successively with alcohol, ether, water, acetic acid, dilute soda solution, and dilute hydrochloric acid. The elasticine is thus purified from other ingredients, but is not itself soluble in either of the above reagents. It is not converted into gelatine even by long boiling; and it is dissolved, but, at the same time, decomposed, only by the concentrated acids and alkalies. The slender elastic fibres mingled with connective tissue, and the sarcolemma of the striped muscular fibres, are probably composed of the same substance.

Keratine.

Under this name is known the exceedingly resisting and indestructible substance of the hair, nails, epidermis, feathers, and all horny tissues. It is unaffected by boiling with alcohol, ether, water, and the dilute acids. By continuous boiling in a Papin's digester at 150° (302° F.) it is liquefied and partly decomposed. It is distinguished from the preceding substance by containing sulphur as an ingredient, which is not present in elasticine. Keratine, accordingly, when decomposed by boiling under pressure or with concentrated alkalies, gives rise to hydrogen sulphide vapors.

It is evident that the albuminous substances, under different forms, constitute a large and important part of the mass of the body; and as they are during life in a constant state of active alteration, they require for their maintenance an abundant supply of similar ingredients in the food. All highly nutritious articles of diet contain more or less of these substances. According to the estimates of Payen, which correspond very closely in their gross results with our own observations, an adult man requires a daily supply of about 130 grammes of albuminous matter to provide for the wants of the system; and this quantity is actually contained in the food consumed.

But although nitrogenous matter is thus abundantly supplied to the system from without, yet the particular kinds of albuminous substances characteristic of the various tissues and fluids are formed within the body in the process of digestion and assimilation, by transformation of

those which are introduced with the food. A large part of the albuminous matters of the food are derived from vegetables, and, though closely related to the corresponding animal substances, are not precisely identical with them. Even the animal albuminous matters used for food, as the albumen of eggs, the caseine of milk, and the substance of muscular flesh, are usually taken in the coagulated form, and suffer still further changes before they become converted into the albumen of the blood. From their subsequent metamorphoses in the act of nutrition they are transformed into the many specific varieties of albuminous matter peculiar to the different tissues and fluids.

Only a very small proportion of these substances is discharged with the excretions. The albuminous ingredients of the perspiration and sebaceous matter, and the mucus of the urinary bladder and large intestine are almost the only ones which find an exit from the body in this way. A minute quantity of albuminous matter is exhaled in a volatile form with the breath, and a little also, in all probability, from the cutaneous surface. But the entire quantity so discharged bears an insignificant proportion to that which is daily introduced with the food. The albuminous substances, accordingly, are decomposed in the interior of the body. They are transformed by the process of destructive assimilation, and their elements are finally eliminated and discharged under other forms of combination.

CHAPTER V.

COLORING MATTERS.

THERE are found, in various parts of the animal body, a number of substances which are distinguished by imparting to the tissues and fluids a distinct and characteristic coloration. Notwithstanding the evident physiological importance of these substances, and the striking character of their optical properties, they have proved in many respects more difficult of study than the other proximate principles; and with regard to several of them our knowledge is still very imperfect. In some instances this is partly due to the comparatively small quantity in which they occur, in others to the extreme readiness with which they are decomposed or altered in the process of separation. In some cases it has been found difficult to decide whether a variation of tint be due to the different proportions of one or more different coloring matters or to the varying degrees of concentration of a single one.

The coloring matters are all nitrogenous compounds, but differ in essential particulars from the albuminous substances. Those which have been most fully examined are known to be crystallizable; and it is possible that all of them might be obtained in a crystalline form, could they be completely separated without decomposition. The most abundant of all, and that which possesses the most important physiological properties, is the red coloring matter of the blood. It appears to be analogous in many respects to the green matter of the leaves and leaf-like organs in the vegetable world. Each of these two coloring matters is the most abundant and widely diffused in its own kingdom, and is distinguished by the identity of its characters in many different species of animals and plants respectively; and while the red coloring matter of the blood, on the one hand, is the agent by which oxygen is absorbed and distributed in the animal body, on the other, it is the green coloring matter of plants by which carbonic acid and water are decomposed and oxygen set free in the act of vegetation. It is believed by many observers that all the coloring matters of the animal body, at least in man and the vertebrate animals, are derived by transformation from the coloring matter of the blood; and although we have no complete experimental evidence that this is true in all cases, yet it is evident that these substances have a close physiological relation with each other, perhaps as distinct and real as that which exists between the various members of the albuminous or saccharine groups.

The organic coloring matters may be conveniently removed from liquids containing them by the action of *animal charcoal;* that is,

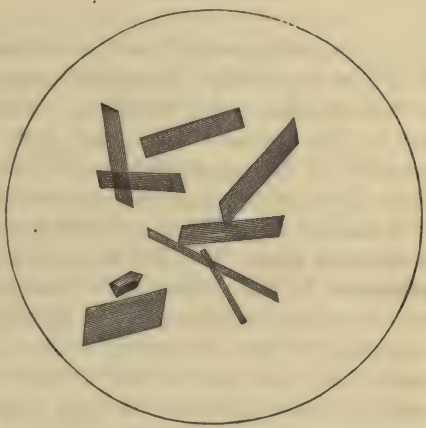
carbon derived from the imperfect combustion of animal substances. Burned bones are generally employed for this purpose, their combustion having been carried on with a scanty supply of air, so that while the hydrogen, nitrogen, and oxygen are driven off in the form of gaseous combinations, the carbon remains behind. If a fluid containing either of the coloring matters be mixed with a sufficient quantity of this charcoal and filtered, the filtered fluid will pass through colorless. Albuminous substances are also retained upon the filter when treated with animal charcoal; while glucose and other crystallizable and saline matters pass through freely in solution.

The animal coloring matters most distinctly recognized are those of the blood, the blackish-brown solid tissues, the bile, and the urine.

Hemoglobine, $C_{900}H_{960}N_{154}Fe,S_3O_{179}$.

This is the coloring matter of the red globules of the blood, the most abundant and important of all the substances belonging to this group. It constitutes much the largest proportion of the solid ingredients of the blood-globules, amounting in all probability to from 25 to 30 per cent. of their weight in the fresh condition. It is also found, in much smaller quantity, in the substance of the muscular tissue, of which it forms the coloring principle. It crystallizes in well marked forms, which vary somewhat in different species of animals; but are all, so far as accurately known, either rhombic or hexagonal tables or prisms. It is soluble in water, in very dilute alcohol, and in dilute solutions of albumen, of the alkalies and their carbonates, and of sodium and ammonium phosphates. It is insoluble in strong alcohol, in ether, and in the volatile and fatty oils. In almost every condition it is readily decomposed. According to Preyer,[1] crystals which have been thoroughly dried at a temperature below the freezing point become, after a time, decomposed, and lose their color and solubility, even at ordinary temperatures. A watery solution of hemoglobine kept at any temperature above 0° (32° F.) becomes altered in the course of twenty-four hours, and if heated to 64° (147° F.) it is at once decomposed.

Fig. 19.



HEMOGLOBINE CRYSTALS; from human blood. (Funke.)

[1] Die Blutkrystalle. Jena, 1871, p. 58.

Hemoglobine, both crystallized and in watery solution, has the clear bright red color of arterial blood. It is distinguished beyond all other known ingredients of the body, by its capacity for absorbing oxygen, which it retains in the form of a loose combination. According to the average result of various experiments one gramme of hemoglobine in watery solution will absorb 1.27 cubic centimetres of oxygen. The oxygen thus absorbed is again given off under the influence of diminished pressure, heat, or the continued displacing action of hydrogen or nitrogen gas. The coloring matter is accordingly known under two different forms, namely, that of "oxidized" hemoglobine, containing an excess of loosely combined oxygen, and that of "reduced" hemoglobine, in which the surplus oxygen has been removed. The color of hemoglobine varies according to these two conditions, being bright red in the oxidized form, and dark purple when deoxidized. The presence of hemoglobine in either one of these two conditions is the cause of the color of arterial and venous blood.

Fig. 20.

HEMOGLOBINE CRYSTALS; from dog-faced baboon. (Preyer.)

A marked feature in the chemical constitution of hemoglobine is that it contains iron. This fact is the more important because it is the only substance in the animal body, excepting hair, which contains iron in any considerable amount, and because iron is also an indispensable requisite for the formation of the green coloring matter of plants. Experiment has shown that without the presence of iron vegetation cannot go on; and there is every reason to believe that iron is equally essential to the constitution of the animal coloring matter, and thus indirectly to the general nutrition of the animal body. It is present in hemoglobine, in all probability, not in the form of a distinct oxide, but directly combined, like sulphur, with the carbon, hydrogen, nitrogen, and oxygen which form the remainder of its substance.

One thousand parts of hemoglobine contain 4.2 parts of iron; and, according to the average results obtained by different observers, healthy human blood contains, per thousand parts, 123.4 parts of hemoglobine, and 0.52 part of iron. This would give, for a man weighing 65 kilogrammes, 2.82 grammes of iron, as contained in the blood of the whole body.

The iron of the hemoglobine passes out of the body by the bile and

the urine, both of which contain slight traces of its presence. It is also contained in the hair, where it forms sometimes as much as 7 per cent. of the incombustible ingredients. It is supplied to the body in ample abundance by ordinary food, in which it is always present in appreciable amount. Green vegetables of course contain it, as an ingredient of their coloring matter. Since hemoglobine exists to some extent in muscular tissue, it will be present in a more or less altered form, but still containing iron, in most kinds of animal food. According to the analyses of Moleschott, 500 grammes of beef (about one pound avoirdupois) will contain 0.035 gramme of iron; and iron is also found in even larger proportion in rye, barley, oats, wheat, peas, and especially in strawberries. As the quantity of this substance daily discharged in the urine and with the bile is so small, we must regard the greater portion of that which passes through the system as used in the growth of the hair; and a very moderate amount contained in the food must be sufficient for the daily requirements of nutrition.

Melanine.

In all the dark-colored tissues of the body, in the choroid coat of the eyeball, the rete Malpighi of the skin in the black and brown races and in all individuals of dark complexion, in the hair, and in the substance of melanotic tumors, there exists a coloring matter known as melanine. When isolated or when collected in compact masses, it is of a very dark blackish-brown color; but by its mixture, in different proportions, with other colorless or ruddy semitransparent elements of the tissues, it may produce all the varying grades of hue, from light yellowish-brown to an almost absolute black. It is deposited in the substance of the animal cells in the form of minute granules, and is usually more abundant in the immediate neighborhood of the nucleus, when one is present, than near the edges of the cell.

Melanine has not yet been obtained in a perfect crystalline form, and its chemical characters are not completely determined. It is known, however, to be a nitrogenous substance. As the average result of various analyses collected by Hoppe-Seyler,[1] it contains, freed from ashes, the following proportions, by weight, of carbon, hydrogen, nitrogen, and oxygen.

Composition of Melanine.

Carbon	54.39
Hydrogen	5.08
Nitrogen	11.17
Oxygen	29.36
	100.00

According to Kühne[2] repeated observations show that it also con-

[1] Handbuch der Physiologisch- und Pathologisch-Chemischen Analyse. Berlin, 1870, p. 177.

[2] Lehrbuch der Physiologischen Chemie. Leipzig, 1868, pp. 365, 442.

tains iron, which has been found in the proportion of 2.5 parts per thousand in the incombustible residue.

Melanine is insoluble in water, alcohol, ether, and solutions of the organic and mineral acids. Boiling solutions of potassium hydrate dissolve it without change of color, but its color is destroyed by chlorine. It is regarded as derived from the coloring matter of the blood, but there is no positive evidence of this, further than the fact that it contains iron, and that it forms the coloring matter of the hair, in which most of the iron of the blood-globules is probably deposited.

Bilirubine, $C_{16}H_{18}N_2O_3$,

The red or orange-red coloring matter of the bile. This substance has been designated, by different writers, under the various names of Biliphæin, Bilifulvine, Hematoidine, and Cholepyrrhine. It is formed in the substance of the liver, and may be extracted from the liver-cells in a pure form. From these it is taken up by the biliary ducts and mingled with the other ingredients of the bile. It is crystallizable, soluble in chloroform, less so in alcohol, and slightly soluble in ether. It is readily soluble also in alkaline liquids, but quite insoluble in pure water. In the crystallized form its color is red; in the amorphous condition, orange; and in solution, reddish-brown or yellow, according to the degree of concentration. According to Hoppe-Seyler, it gives a perceptible yellow color when viewed in a layer of 1.5 centimetre's thickness, even if dissolved in 500,000 times its weight of fluid.

Solutions of bilirubine exhibit a well-marked reaction with nitroso-nitric acid, which is known as "Gmelin's bile test." If to such a solution we add a small quantity of nitric acid, in which nitrous acid is also present, a series of colors is produced in the following order: green, blue, violet, red, and finally a dingy yellow. These colors are produced by transformation of the bilirubine, and represent successive degrees of its oxidation by nitric acid. The reaction is a very sensitive one, and, according to Hoppe-Seyler, will produce a visible result in solutions containing only one part in 70,000.

Bilirubine is generally regarded as derived from hemoglobine. The reasons for this opinion are: First, its reddish color, similar, in some degree, to that of diluted blood. Secondly, it has been found in various parts of the body, in old bloody extravasations, evidently produced from an alteration of the blood upon the spot. When found under these circumstances, it was formerly known as *hematoidine*. Thirdly, if hemoglobine, in the living animal, be withdrawn from the blood-globules, and made to assume a liquid form by alternately freezing and thawing a portion of freshly drawn blood, and then re-injected into the bloodvessels, this operation is followed by a discharge of bilirubine with the urine. If hemoglobine, however, be normally transformed into bilirubine, its iron and sulphur must enter into some other combination, as neither of these substances exists in the coloring matter

of the bile. Bilirubine, if exposed to the atmospheric air in alkaline solution, becomes oxidized and assumes a green color, being converted into another closely related substance, namely, biliverdine.

Biliverdine, $C_{16}H_{20}N_2O_5$.

In addition to bilirubine, the bile contains also a green coloring matter, namely, biliverdine; and its varying tint in different specimens depends on the different proportions in which the two substances are present. In many species of animals, as in the ox, sheep, rabbit, and vegetable feeders generally, the bile presents a strong green or greenish color, due to the comparative abundance of biliverdine. Biliverdine is insoluble in water, ether, and chloroform, readily soluble in dilute alkaline solutions and in alcohol. It is also soluble in glacial acetic acid, and is deposited from the evaporated solution in the form of an imperfect crystallization. It is often found in human gall-stones, and in the dog is abundantly deposited along the edges of the placenta.

There is every reason to believe that biliverdine is formed from bilirubine by a process of oxidation, the elements of water entering at the same time into combination. The nature of this change is shown by the following formula:

$$\underset{\text{Bilirubine.}}{C_{16}H_{18}N_2O_3} + H_2O + O = \underset{\text{Biliverdine.}}{C_{16}H_{20}N_2O_5}.$$

The prompt conversion of the color of ruddy or reddish-brown bile into green by the action of various oxidizing agents, or even by exposure to the air, and the evident chemical relationship between the two substances, leave no doubt that this is the mode in which biliverdine originates in the animal body. Both bilirubine and biliverdine are discharged with the bile into the alimentary canal, but they become undistinguishable toward the lower end of the small intestine. Beyond that point they are replaced by the brown coloring matter of the feces, and are finally discharged from the body under this form.

Urochrome.

The coloring matter of the urine has been repeatedly studied by competent and laborious observers, but thus far with only partial success. The substances which have been extracted from the urine by various methods, and which have been regarded as representing, more or less exactly, its natural coloring principle, are known by the different names of Urochrome, Urosine, Urosacine, Hemaphæine, Urohematine, Uroxanthine, Urobiline, and Hydrobilirubine. They are all probably modifications of the same substance, variously altered by different methods of extraction, or obtained in different grades of purity. The fresh, normal urine has a light yellowish or amber color, while specimens of unusually high specific gravity, and particularly specimens of febrile urine, often exhibit a distinct reddish hue. Normal urine, which, when fresh, is only amber-colored, will often, by exposure to the air, acquire a tinge of red. The substance obtained by Thudi-

chum,[1] and called by him urochrome, is precipitable from the urine by various metallic salts. It has not yet been produced in a crystalline form. It is soluble in water and in ether, but only slightly soluble in alcohol. Its watery solution has a yellowish color, which, on standing, becomes red. *Urohematine* (Harley) is nitrogenous in composition, and contains iron.[2] It is insoluble in pure water, but soluble in the fresh urine, as well as in ether, chloroform, and alcohol. The substance termed *Urobiline* (Jaffé) was so named because supposed to be derived from the coloring matters of the bile. It is soluble in alcohol, ether, and chloroform. Its solutions have a brownish-yellow color, and, by dilution, become first yellow, and lastly faint rosy-red. It was found by Jaffé[3] to be present in nearly every instance (45 cases) in healthy human urine, where it was recognized, after partial extraction and purification, by its peculiar optical (spectroscopic) properties. The same observer, however, found that fresh urine, not subjected to chemical manipulation, would often present no indication of urobiline. Such urine, if secluded from the atmosphere, would remain light-colored, and free from this substance; but if exposed to the air for from two to twelve hours, would become darker in hue, and at the same time would show, by the spectroscope, signs of the presence of urobiline.

It is evident, therefore, that the urine contains a coloring matter which gives to it in the fresh condition its well known amber tint. This substance is liable to be changed under the influence of oxidation, and to assume in that condition a more or less distinct red color. Such a modification certainly takes place outside the body, and it is possible that it may also occur within the system, giving rise to the varying proportions of red in the color of the urine in different healthy and diseased conditions.

Beside the above named substances, there are two other bodies of sufficient interest in general physiology to be enumerated in connection with those already described.

Luteine.

This substance, as its name indicates, is of a strongly marked yellow color. It is extracted from the yolk of eggs, and from the tissue of the corpus luteum. It exists also, according to Thudichum,[4] in the grains of Indian corn, in certain berries and roots, and in the yellow stamens and petals of a large number of flowering plants. It is crystallizable, soluble in alcohol, ether, chloroform, and the fatty oils, but insoluble in water. It is readily decomposed and decolorized by sunshine; and by the action of nitric acid it is first turned blue, and afterward decolorized.

[1] British Medical Journal, London, Nov. 5, 1864.

[2] Harley, The Urine and its Derangements. Philadelphia, 1872, p. 97.

[3] Archiv für Pathologische Anatomie und Physiologie, 1869, vol. xlvii. p. 405.

[4] Centralblatt für die Medicinische Wissenschaften, 1869, p. 2.

Its color is also changed to blue or green by other strong acids, but it is not affected by dilute solutions of the alkalies. It has not yet been obtained in sufficient quantity for complete analysis.

Chlorophylle.

This is the green coloring matter of plants. It is more widely diffused than any other coloring matter in the vegetable world, and it apparently constitutes exclusively the coloring principle of all the green parts of the higher plants without exception. Its exact chemical constitution has not been fully determined, but it is considered to be a nitrogenous substance, and Mulder has given it the formula $C_9H_9NO_4$. It is certain that iron is essential to its production, as plants artificially cultivated without the access of this substance, grow up in a blanched or chlorotic condition; and their green color may afterward be restored by the supply of moisture containing a ferruginous salt.[1]

Chlorophylle is of the first importance in vegetable physiology, as it is under the influence of this substance, together with that of the solar light, that the inorganic ingredients of the soil and the atmosphere are deoxidized and combined in the form of an organic carbo-hydrate. The process of vegetation proper, that is, the production and accumulation of organic material in the form of starch, sugar, cellulose, woody fibre, and the substance of various vegetable tissues, is inseparably dependent on the presence and action of chlorophylle. At the same time, in order to produce this effect, the chlorophylle must constitute a part of the living vegetable cell; for the coloring matter alone, if extracted from the chlorophylle-holding cells, and placed under all other conditions, such as the access of air, sunlight, warmth, and moisture, known to be essential to the work of production, is found to be incapable of forming organic matter out of water and carbonic acid. Its function, therefore, is not that of a simple chemical reagent, but that of an active constituent of the living vegetable organism.

Chlorophylle is produced, in the interior of the vegetable cell, sometimes as a uniformly diffused mass. Usually, however, it is deposited in the form of distinct rounded grains, frequently arranged in definite figures or patterns in the cavity of the cell. It may be extracted by the action of alcohol or of ether, and retains its green color in solutions of these substances. It disappears previously to the shedding of the leaves, when they cease to perform the act of vegetation, and is usually replaced by a few grains of red or yellowish color.

[1] Mayer, Lehrbuch der Agrikultur-Chemie, Band i. pp. 51, 265.

CHAPTER VI.

CRYSTALLIZABLE NITROGENOUS MATTERS.

THE fifth and last group of proximate principles consists of a number of colorless substances which, like the albuminous matters, contain nitrogen, but which differ from them in being readily crystallizable. Many of them are evidently derived from the albuminous ingredients of the body by retrograde metamorphosis, being discharged from the system as products of excretion. Others do not exhibit this character, and are found only in the permanent tissues or the internal fluids of the body. Several of them are of comparatively recent discovery, and, although undoubtedly of importance in the constitution of the body, are still somewhat obscure in their physiological relations.

Lecithine, $C_{44}H_{90}NPO_9$,

From Λέκιθος, the yolk of egg, in which substance it was first discovered. Lecithine was for some time described under the name of *phosphorized fat*, owing to the circumstance that one of the products of its decomposition is phosphoglyceric acid ($C_3H_9PO_6$). It is not, however, a fatty substance, since it contains nitrogen, and in other respects differs from the fats. As mingled or combined with other animal matters, it has also been known by the name of "protagon." Lecithine is of very wide distribution in both the animal and vegetable kingdoms, occurring in the cereal grains and the leguminous seeds, and, according to Hoppe-Seyler, in the cellular juices of a variety of plants. It is found in the blood, both in the plasma and the globules, in the bile, the spermatic fluid, the yolk of egg, and particularly in the tissues of the brain, spinal cord, and nerves. In the plasma of the blood, it is in the proportion of 0.4 part per thousand, and in the fresh substance of the calf's brain, according to the analyses of Petrowsky,[1] in the proportion of 31 parts per thousand. Taking into account the watery ingredients of the brain, lecithine is about equally abundant in the white and gray substance; but of the solid matters alone, it constitutes a little less than 10 per cent. in the white substance, and rather more than 17 per cent. in the gray substance.

Lecithine obtained from either of these sources, if treated with water, swells up into a pasty mass and gives origin to the remarkable appearances under the microscope known as "myeline forms;" that is, a great

[1] Archiv für die gesammte Physiologie, 1873, Band vii. p. 101.

variety of mucilaginous or oily looking drops and filaments, of double contour, which exude from the edges of the mass, and remain separate and insoluble; resembling the microscopic forms produced under similar circumstances from the "myeline," or medullary layer of nerve fibres. It is readily soluble in alcohol, less so in ether, and is also soluble to some extent in chloroform and the fatty oils. It is readily decomposed on standing, either in solution or in a state of watery imbibition, acquiring an acid reaction. Decomposition is also effected by the action of acids or alkalies. By boiling with baryta water it suffers a characteristic alteration, giving rise to the production of two new bodies; namely, a nitrogenous alkaline substance and phosphoglyceric acid.

Lecithine has a special importance, not only as an abundant ingredient of the nervous tissue, but also as being the only organic combination in the body containing phosphorus. Considering the number of vegetable and animal articles of food in which it is an ingredient, it is evident that a considerable quantity must be introduced with the nutriment into the system and assimilated by the tissues, particularly by those of the nerves and nervous centres. But as no known organic combination of phosphorus is discharged with the excretions, this substance must pass out of the body as part of the phosphates which appear in the urine and the perspiration. On this account, together with the known fact of the constant consumption of oxygen by the animal body, it is believed that the phosphorus, introduced as an ingredient of organic materials, is converted by oxidation in the system into phosphoric acid, and thus appears finally under the form of phosphatic salts.

Cerebrine, $C_{17}H_{33}NO_3$.

As its name indicates, this is an ingredient of the brain and nerves, the only healthy constituents of the body in which it is known to exist. Although this substance has not been obtained in a crystalline form, it is placed among the members of this group because it resembles them in the general features of its chemical composition, particularly in its small proportion of nitrogen, and also in certain of its reactions, which are entirely dissimilar to those of an albuminous matter.

Cerebrine is insoluble in water, but if moistened swells up slowly into a pasty mass. It is insoluble in ether and in cold alcohol.

It is readily soluble in boiling absolute alcohol, from which it is again deposited on cooling. Boiling with baryta water decomposes it very slowly and incompletely, and does not produce phosphoglyceric acid, by which means it may be distinguished from lecithine. If strongly heated in the air, it turns brown, melts, and finally burns with a bright flame.

It is much more abundant in the white than in the gray substance of the brain, forming, according to Petrowsky, in the solid ingredients of the white substance 9.5 per cent., in those of the gray substance but

little more than 0.5 per cent. It is, therefore, undoubtedly a constituent of the medullary layer of nerve fibres.

Leucine, $C_6H_{13}NO_2$,

So called from the glistening white color of its crystals. It is found in the tissue of the spleen, the thymus, thyroid, lymphatic, submaxillary, and parotid glands, the pancreas and pancreatic juice, the brain, liver, kidneys, and supra-renal capsules. In all these situations it exists in comparatively small quantity, but its exact proportions have not been determined. It has not yet been found in the blood in a state of health, and has only been met with in the urine in certain cases of disease. According to Hoppe-Seyler it is one of the products of putrefactive decomposition of albuminous and gelatinous substances. When pure, it crystallizes in thin white laminæ, in which form it is readily soluble in water, less so in alcohol, and insoluble in ether. Heated slowly to 170° (338° F.) it volatilizes unchanged; above this point it is decomposed; two of the products of its decomposition being carbonic acid and ammonia. But little is known with regard to the normal origin or physiological destination of this substance, its importance being only indicated by the number and variety of the situations in which it is found.

Sodium Glycocholate, $C_{26}H_{42}NO_6Na$.

This is one of the characteristic ingredients of the bile, where it sometimes forms, according to the observations of Jacobsen, nearly 49 per cent. of the dry residue. It is also found in the tissue of the liver and in the fluids of the upper part of the intestinal canal, into which it is discharged with the bile; but it does not exist in the blood or in the other animal fluids.

It is a saline body, consisting of a nitrogenous organic acid, glycocholic acid ($C_{26}H_{43}NO_6$) in combination with sodium. Glycocholic acid is so called because by boiling with solutions of potassium hydrate or baryta water, or by continued boiling with dilute hydrochloric or sulphuric acids, it is decomposed with the production of two new bodies, namely, *glycine* ($C_2H_5NO_2$), a nitrogenous neutral substance, and *cholic acid* ($C_{24}H_{40}O_5$), a non-nitrogenous organic acid, so called because peculiar to the bile. This change takes place with the assumption, by the glycocholic acid, of the elements of water, as follows:

$$\underset{\text{Glycocholic acid.}}{C_{26}H_{43}NO_6} + H_2O = \underset{\text{Glycine.}}{C_2H_5NO_2} + \underset{\text{Cholic acid.}}{C_{24}H_{40}O_5}.$$

The two bodies thus formed do not, therefore, pre-exist in the organic acid of the bile, but are produced, by the addition of other elements, at the time of its decomposition.

Sodium glycocholate is a neutral, crystallizable substance, very soluble in water and in alcohol, and insoluble in ether. It is accordingly extracted from the bile by the following process: The bile is first evaporated to dryness over the water-bath, the dry residue extracted

with absolute alcohol, the alcoholic solution decolorized with animal charcoal, and then mixed with from 8 to 10 times its volume of ether. A whitish precipitate is thrown down which soon collects into little drops and masses, of a consistency like that of Canada balsam, whence the biliary salts have been sometimes termed the "resinous" matters of the bile. In the course of 24 hours, sometimes only after four or five days, the sodium glycocholate crystallizes abundantly in the form of hemispherical or star-shaped masses of fine radiating acicular crystals. These crystals may be preserved indefinitely in the mixture of alcohol and ether; but if the mixture be poured off, the cold produced by evaporation causes a condensation of atmospheric moisture and a rapid melting and solution of the crystals, which may be seen under the microscope liquefying into transparent, rounded, oleaginous-looking drops. The solubility of these drops in water and their insolubility in ether will readily distinguish them from oil globules, which they closely resemble in their optical properties. Sodium glycocholate may be precipitated from its watery solution by both the neutral and tribasic lead acetates. Its alcoholic solution rotates the plane of polarization toward the right 25°.7.

Fig. 21.

SODIUM GLYCOCHOLATE FROM OX-BILE, after two days' crystallization. At the lower part of the figure the crystals are melting into drops, from evaporation of the ether and absorption of moisture.

Sodium Taurocholate, $C_{26}H_{44}NSO_7Na$.

This is a substance similar in many of its properties to the last, and, like it, a peculiar ingredient of the bile. Its organic acid, taurocholic acid ($C_{26}H_{45}NSO_7$), is distinguished by containing an atom of sulphur, owing perhaps to its having been derived from the albuminous matters. If so, glycocholic acid will represent a product of further oxidation, under which sulphur, hydrogen, and oxygen are given up in such proportions that the products of elimination are sulphuric acid and water, as follows:

$$\underset{\text{Taurocholic acid.}}{C_{26}H_{45}NSO_7} - S(H_2O) = \underset{\text{Glycocholic acid.}}{C_{26}H_{43}NO_6}.$$

By boiling with dilute acids or alkalies, or even in water, taurocholic acid is decomposed with the formation of two other bodies, namely, *taurine* ($C_2H_7NSO_3$), a neutral nitrogenous substance, containing all the sulphur, so called because first discovered in bullock's bile, and *cholic acid*

($C_{24}H_{40}O_5$), the same body produced by a similar process from glycocholic acid. The change here also takes place with the assumption of the elements of water, as follows:

$$\underset{\text{Taurocholic acid.}}{C_{26}H_{45}NSO_7} + H_2O = \underset{\text{Taurine.}}{C_2H_7NSO_3} + \underset{\text{Cholic acid.}}{C_{24}H_{40}O_5}.$$

Fig. 22.

SODIUM TAUROCHOLATE, from alcoholic extract of dog's bile, crystallizing at the bottom of a test-tube.

Sodium taurocholate, like the preceding biliary salt, is soluble in water and in alcohol, and insoluble in ether. It is extracted from the bile by a similar process to that already described, and, after precipitation by ether, crystallizes in slender needles, much like those of the glycocholate. It may be distinguished, however, and separated from the last-named substance, when in company with it, by its reaction toward the salts of lead. It is not precipitated from its watery solution by the neutral, but only by the tribasic acetate. If a watery solution, therefore, containing both salts be precipitated by neutral lead acetate, the filtered fluid will contain the sodium taurocholate alone. In alcoholic solution it rotates the plane of polarization toward the right 24°.5.

The two biliary salts are associated in the bile in varying proportions. Generally the glycocholate may be said to preponderate in the bile of the ruminant animals, taurocholate in that of the carnivora. In dog's and cat's bile, the taurocholate exists alone. In human bile it appears that both substances may be present, sometimes one of them being the more abundant, sometimes the other; according to some writers the taurocholate existing alone or in larger proportion (Gorup-Besanez, Hoppe-Seyler, Robin, Hardy), according to others the glycocholate (Bischoff, Lossen, Ranke). In the observations of Jacobsen,[1] on a case of biliary fistula in man, the glycocholate was shown to be a constant ingredient, while the taurocholate was either absent, or, if present, varied in quantity. We have also found human bile to contain the glycocholate without the presence of taurocholate.

The biliary salts are formed in the glandular tissue of the liver and discharged with the bile. According to the observations of Ranke on a man with biliary fistula, the average quantity of the organic acids of the bile thus produced, by a man weighing 65 kilogrammes, would be a little over 15 grammes per day. They are not discharged with the feces, but are changed in the intestine, and, probably, reabsorbed under another form by the blood.

Creatine, $C_4H_9N_3O_2$, from κρέας, flesh.

This is a neutral crystallizable substance, which exists very generally in the muscular tissue, both voluntary and involuntary, of man and

[1] Revue des Sciences Médicales, 1874, vol. iii. p. 85.

animals; its proportion in the human muscles being, according to Neubauer,[1] about two parts per thousand. It has also been found in minute quantity in the blood, the brain, and the kidneys. It is soluble in cold, very readily in hot water, slightly soluble in alcohol, insoluble in ether. From its watery solution it crystallizes in the form of transparent, colorless, rhombic prisms of firm consistency. It is decomposed by a temperature of 100° (212° F.). By boiling in acid solutions, or by long-continued boiling in water, it is transformed into another closely related substance, namely, creatinine. If boiled with baryta water it produces, among other substances, urea, carbonic acid, and ammonia. Creatine is regarded as a product of metamorphosis of the albuminous matters, especially of those existing in muscular tissue. It does not appear in the urine, but undergoes further transformation in the interior of the body, probably into the following substance.

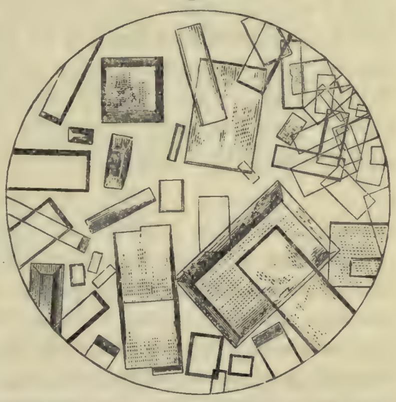
Fig. 23.

CREATINE, crystallized from hot water. (Lehmann.)

Creatinine, $C_4H_7N_3O$,

Is known to exist, with certainty, only in the urine. Although it has been occasionally found by some observers in the muscles, according to Neubauer it is not a normal ingredient of the tissue, but is produced during the process of extraction, under the continued influence of heat and moisture, from the previously existing creatine. Creatinine is soluble in water and in alcohol, but only slightly soluble in ether. It crystallizes in colorless glittering prisms. In solutions it has a strong alkaline reaction, decomposes the combinations of ammonia, and forms with various acids neutral salts.

Fig. 24.



CREATININE, crystallized from hot water. (Lehmann.)

The relation between these two bodies is such that by different chemical processes they may be artificially converted into each other. In the interior of the body

[1] Neubauer und Vogel, Analyze des Harns, 1872, p. 20.

the change which takes place is undoubtedly the conversion of creatine into creatinine, since the former is that which exists normally in the muscles, while the latter is an ingredient of the urine. In this change the elements of water are eliminated as follows:

$$\underset{\text{Creatine.}}{C_4H_9N_3O_2} - H_2O = \underset{\text{Creatinine.}}{C_4H_7N_3O}.$$

Thus creatine represents an intermediate stage of the products of metamorphosis, which finally appear in the urine under the form of creatinine. According to the observations of Neubauer, the quantity of creatinine discharged by a healthy man, under ordinary diet, is about 1 gramme per day.

Urea, CH_4N_2O.

This is one of the most important and well known substances of its class, as it is the principal solid ingredient of the urine, and the main product of the decomposition of nitrogenous matters in the body. It is most abundantly found in the urine, where it is present on the average, in man, in the proportion of 26 parts per thousand; while in the blood it is only in the proportion of 0.16 part per thousand. As it makes its appearance in the blood, it is constantly drained away by the kidneys, and thus accumulates in larger proportion in the urine. This is further shown by the comparative analyses of Picard, who found, in the dog, the proportion of urea in the blood of the renal arteries to be 0.36 per thousand, in the renal veins 0.18 per thousand. Urea has also been found in minute quantity in the lymph, the aqueous and vitreous humors of the eye, the crystalline lens, and the perspiration.

Urea is a colorless, neutral substance, abundantly soluble in water and in boiling alcohol, less so in cold alcohol, nearly insoluble in ether. It crystallizes in four-sided prisms, often with blunt pyramidal ends, which are decomposed on being heated above 120° (248° F.). Its pure watery solution may be kept without change at ordinary temperatures; but by long continued boiling, or by a short boiling in the presence of alkalies, it is decomposed with the production of ammonium carbonate. If heated with water in an hermetically sealed tube to 180° (356° F.), it undergoes the same alteration. This change takes place with the assumption of the elements of water, as follows:

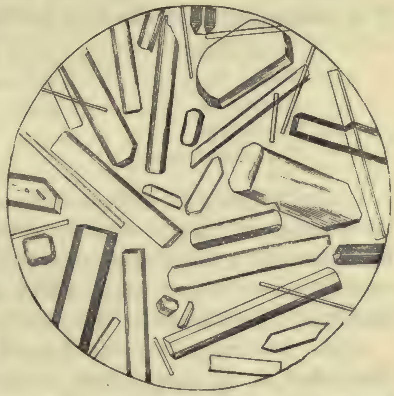
$$\underset{\text{Urea.}}{CH_4N_2O} + H_4O_2 = \underset{\text{Ammonium carbonate.}}{(NH_4)_2CO_3}.$$

Urea has been produced artificially from albuminous matter, by placing the latter in contact with potassium permanganate in watery solution, and subjecting it to a heat of 60° to 80° (140° to 176° F.). This reaction, first established by Béchamp,[1] has been confirmed by Ritter,[2] in whose experiments 30 grammes of albumen furnished 0.09 gramme of urea, and the same quantity of fibrine, 0.07 gramme;

[1] Comptes Rendus de l'Académie des Sciences, Paris, 1870, tome lxx. p. 866.
[2] Comptes Rendus, 1871, lxxiii. p. 1219.

while from 30 grammes of gluten, in an average of three experiments, there was obtained 0.27 gramme of urea. According to Béchamp, this is not a process of simple oxidation, but an oxidation with decomposition, in which various other substances are produced from the albuminous matter at the same time with urea. The quantity of urea excreted by a healthy man is about 35 grammes per day. This amount varies, of course, with the size of the body, the average daily proportion of urea to the weight of the whole body being 0.5 per thousand parts. Lehmann, in experiments on his own person, found the average daily quantity to be 32.5 grammes. Bischoff, by similar experiments, found it to be 35 grammes. Prof. William A. Hammond, whose weight was 90 kilogrammes, found it to be 43 grammes. Prof. John C. Draper, whose weight was 66 kilogrammes, found it 26.5 grammes.

Fig. 25.



UREA, prepared from urine, and crystallized by slow evaporation. (Lehmann.)

It has been shown by Prof. John C. Draper,[1] and confirmed by other observers, that there is a *diurnal* variation in the normal quantity of urea. A smaller quantity is produced during the night than during the day; and this difference exists even in patients who are confined to the bed during the whole twenty-four hours, as in the case of a man under treatment for fracture of the leg. This is probably owing to the greater activity, during the waking hours, of both the mental and digestive functions. More urea is produced in the latter half than in the earlier half of the day; and the greatest quantity is discharged during the four hours from 6½ to 10½ P. M.

The quantity of excreted urea represents almost completely the amount of decomposition in the nitrogenous organic ingredients of the body; since it is the only nitrogenous substance discharged in considerable quantity by the excretions. A comparison of the entire amount of nitrogen contained in the daily food with that discharged from the body in various forms shows that fully 85 per cent. of that introduced reappears as an ingredient of the urea; the remaining 15 per cent. being contained in the uric and hippuric acids and creatinine of the urine, and in the nitrogenous matters of the feces.

All observers are agreed that the quantity of urea excreted varies in proportion to the amount of nitrogenous matters contained in the food.

[1] New York Journal of Medicine, March, 1856.

Lehmann found,[1] in experiments on his own person, that the daily amount of urea was increased by a diet of animal food, diminished by one of vegetable food, and reduced to its minimum by a diet consisting exclusively of non-nitrogenous matters, such as starch, sugar, and fat. The comparative results were as follows:

Kind of diet.	Daily quantity of urea.
Mixed	32.5 grammes.
Animal	53.2 "
Vegetable	22.5 "
Non-nitrogenous	15.4 "

It also appears from the observations of Mahomed[2] that the influence of a change of diet in this respect is manifested very rapidly; twenty-four hours of a non-nitrogenous diet being sufficient to reduce the excretion of urea 50 per cent., while it is again restored to its ordinary standard within three or four hours after the use of animal food.

Urea, however, does not depend exclusively upon the direct transformation of the nitrogenous matters of the daily food, but is also, in part at least, derived from the metamorphosis of the more permanent constituents of the body; since it continues to be discharged, though in diminished quantity, when no food is taken. Lehmann found as much urea in the urine after twenty-four hours of abstinence from all food, as after a diet of non-nitrogenous matters. In the dog, when subjected to entire abstinence, the urea is reduced in three or four days to nearly one-third its former quantity, but is still present in about the same proportion at the end of seven days. In the experiments of Dr. Parkes on a man subjected to a purely non-nitrogenous diet, the daily excretion of urea fell on the second day to 12 grammes, but afterward remained nearly uniform, at rather more than half that quantity, and on the fifth day still amounted to 7 grammes. Urea has also been found by Lassaigne in the urine of man after continued abstinence from food for fourteen days.

The quantity of urea has been found by Lehmann,[3] Prof. A. Flint, Jr.,[4] Parkes,[5] and Vogel[6] to be increased during or after unusual muscular exertion. Other observers (Fick and Wislicenus, Voit, Ranke) have found no perceptible variation owing to this cause. The same discrepancy exists between different writers in regard to creatinine. It is possible that the details of the process by which the albuminous matters during decomposition give rise to the formation of urea are not yet fully known to us. But it is a matter of common experience, both for man and animals, that continued and laborious muscular activity

[1] Physiological Chemistry. Sydenham edition. London, 1853, vol. ii. p. 450.
[2] Pavy on Food and Dietetics. Philadelphia edition, 1874, pp. 79–81.
[3] Physiological Chemistry. Sydenham edition, vol. ii. p. 452.
[4] New York Medical Journal, June, 1871.
[5] Proceedings of the Royal Society, March 2d, 1871, p. 357.
[6] Neubauer und Vogel, Analyse des Harns, 1872, p. 338.

requires a corresponding supply of nitrogenous food; and the final result of the internal metamorphosis of such substances is mainly represented by the excretion of urea.

Sodium Urate, $C_5H_3N_4O_3Na$.

As its name indicates, this is a saline body, consisting of a nitrogenous organic acid, namely, *uric acid* ($C_5H_4N_4O_3$), in union with sodium. A portion of it is also in combination with potassium, but the sodium salt is in much the greater quantity of the two. The urates are found normally only in the urine, where they exist in the proportion of about 1.45 parts per thousand. The entire quantity of uric acid excreted by a healthy, full-grown man, is about 0.7 gramme per day. It is, therefore, very much less abundant than urea; and, according to the researches of J. Ranke, the proportion between them is very constant, the relative daily quantity of the two substances in the same individual being nearly always—

Uric acid	1 part.
Urea	45 parts.

Uric acid is a colorless, crystallizable substance, only very slightly soluble in either cold or hot water, quite insoluble in alcohol and in ether. It is much less easily decomposed than urea, remaining for a long time unchanged under all ordinary conditions. If treated with concentrated sulphuric acid it is decomposed, with the production of ammonia and carbonic acid. If boiled with dilute nitric acid, it dissolves with a yellow color and abundant liberation of gas-bubbles; and, on evaporation, the solution leaves a brilliant red stain, which is changed to purple by the addition of a drop of ammonia water. This is known as the "murexide test" for uric acid or the urates.

Uric acid, like urea, is formed within the body by the metamorphosis of nitrogenous organic substances. It is most abundant under the use of animal food, and diminished by a vegetable diet, and is reduced to a minimum, though it does not entirely disappear, during complete abstinence. It is this substance which indirectly, in great measure, causes the acid reaction of the urine. It is nowhere present normally in a free form, being by itself exceedingly insoluble; but simultaneously with its production it unites with part of the alkaline bases of the phosphates, thus becoming mainly sodium urate, which is soluble and neutral in reaction, and giving rise to sodium biphosphate, which communicates to the urine its acid reaction.

Sodium Hippurate, $C_9H_8NO_3Na$.

This is also a saline body, formed by the union of sodium with a nitrogenous organic acid, namely, *hippuric acid*, $C_9H_9NO_3$, so called because it was first discovered in the urine of the horse. It is comparatively abundant in the urine of most herbivorous animals, especially the horse, ox, sheep, goat, elephant, camel, and rabbit; while it is

absent, or nearly so, in that of the carnivorous animals. In human urine, under an ordinary mixed diet, it is constantly present, amounting to about 0.35 gramme per day, or about one-half the quantity of uric acid. It increases, however, perceptibly under a vegetable diet, and diminishes or disappears altogether under the exclusive use of animal food. It thus alternates in quantity, under these circumstances, with uric acid. In the urine of the horse, which normally contains hippuric acid, after continued abstinence from food, this substance ceases to appear, and uric acid takes its place. Herbivorous animals, when deprived of food, are placed in the condition of carnivora, since the ingredients of the urine must then be derived from the metamorphosis of their own substance. In the calf, while living upon the milk of its dam, the urine contains uric acid; after the animal is weaned and begins to live upon vegetable food, the uric acid disappears, and the urine contains salts of hippuric acid.

CHAPTER VII.

FOOD.

Under the term "food" are included all substances, both solid and liquid, necessary to sustain the process of nutrition. The first act of this process is the appropriation from without of the materials which enter into the composition of the living frame, or of others which may be converted into them in the interior of the body. Like the tissues and the fluids, therefore, the food contains various ingredients, both organic and inorganic; and the first important fact to be noted with regard to them is that *no single class of substances, by itself, is sufficient to sustain life*, but that several must be supplied, in due proportion, in order to maintain the body in a healthy condition.

Inorganic Ingredients of the Food.

It is well known that inorganic substances, although they afford the necessary materials for vegetation, are not sufficient for the nourishment of animals, which depend for their support upon elements already combined in the organic form. Nevertheless, it is equally true that the inorganic matters are also essential to animal life, and require to be supplied in sufficient quantity to keep up the natural proportion in which they exist in the various solids and fluids. As we have found it to be a general characteristic of these substances, that they are exempt from alteration in the interior of the body, but are absorbed, deposited, and expelled unchanged, each one, as a rule, requires to be present under its own form, and in sufficient quantity in the food. This is especially true of water and sodium chloride, both of which enter and leave the system in abundant daily quantity; and of the calcareous salts, which during the growth and ossification of the skeleton are deposited in large proportion in the osseous tissue. The alkaline carbonates, phosphates, and sulphates are partly formed within the system during the metamorphosis or decomposition of organic substances; but the elements of which they are composed must of course enter the body in some form, in order to enable these changes to be accomplished.

Since water enters into the composition of every part of the body, it is important as an ingredient of the food. In man, it is probably the *most* important substance to be supplied with constancy and regularity, and the system suffers more rapidly when entirely deprived of fluids, than when the supply of solid food only is withdrawn. A man may pass eight or ten hours without solid food, and suffer little or no inconvenience; but if deprived of water for the same length of time,

he becomes exhausted, and feels the deficiency in a marked degree. Magendie found, in his experiments on dogs subjected to inanition,[1] that if the animals were supplied with water alone they lived six, eight, and even ten days longer than if deprived at the same time of both solid and liquid food. Sodium chloride, also, is usually added to the food in considerable quantity, and requires to be supplied as a condiment with tolerable regularity; while the remaining inorganic materials, such as the calcareous salts, and the alkaline phosphates and sulphates, occur naturally in sufficient quantity in most of the articles used as food.

The entire quantity of mineral substances discharged daily by a healthy adult, by both the urine and perspiration, averages as follows:

QUANTITY OF MINERAL MATTERS DISCHARGED PER DAY.

Sodium and potassium chlorides	15.0	grammes.
Calcareous and magnesian phosphates	1.0	"
Sodium and potassium phosphates	4.5	"
Sodium and potassium sulphates	4.0	"
	24.5	"

According to the average dietaries for adults in full health collected by Dr. Playfair[2] about 20 grammes of mineral matter are daily introduced with the food. The remainder is to be accounted for by the phosphates and sulphates formed within the system as above described.

Non-Nitrogenous Organic Ingredients of the Food.

These substances, so far as they enter into the composition of the food, are divided into the two natural groups already mentioned—namely, the *carbohydrates*, including starch and sugar, and the *fats*, including all the varieties of oleaginous matter. Since starch is always converted into glucose in the digestive process, these two substances have the same value and significance as nutritive materials. As the carbohydrates are to be found as a general rule only in vegetable products, they do not constitute a part of the food of carnivorous animals. It is true that glucose exists in the milk even of the carnivora during lactation, and is consequently supplied as a nutritive material to the young animal during the early portion of its growth. But this supply ceases as soon as the period of lactation is finished; and the fact of the secretion of sugar by the mammary gland, as well as that of its production in the liver, shows that in the carnivorous animal the carbohydrates requisite for the process of nutrition may originate within the body from other organic substances. This does not apply, however, to the vegetable feeders or to man. The carnivora have no desire for vegetable food, while the herbivora live upon it exclusively, and in man there is a natural craving for it, which is almost universal. It may be dis-

[1] Comptes Rendus de l'Académie des Sciences. Paris, tome xiii. p. 256.
[2] London Chemical News, May 12, 1865.

pensed with for a few days, but not indefinitely. The experiment has often been tried, in the treatment of diabetes, of confining the patient to a strictly animal diet. It has been invariably found that, if this regimen be continued for some weeks, the desire for vegetable food becomes so imperative that the plan of treatment is unavoidably abandoned.

A similar question has arisen with regard to the oleaginous matters. Are these substances indispensable as ingredients of the food, or may they be replaced by other proximate principles, such as starch or sugar? It has already been seen, from the experiments of Boussingault and others, that a certain amount of fat is produced in the body over and above that which is taken with the food; and it appears also that a regimen abounding in saccharine substances is favorable to the production of fat. It is altogether probable, therefore, that the materials for the production of fat may be derived, under these circumstances, either directly or indirectly from saccharine matters. But saccharine matters alone are not sufficient. Dumas and Milne-Edwards[1] found that bees, fed on pure sugar, soon cease to work, and sometimes perish in considerable numbers; but if fed with honey, which contains some waxy and other matters beside the sugar, they thrive upon it; and produce, in a given time, a much larger quantity of fat than was contained in the whole supply of food.

The same thing was established by Boussingault with regard to starchy matters. He found that in fattening pigs, though the quantity of fat accumulated by the animal considerably exceeded that contained in the food, yet fat must enter to some extent into the composition of the food in order to maintain the animal in good condition; for pigs, fed on boiled potatoes alone (an article abounding in starch but nearly destitute of oily matter), fattened slowly and with difficulty; while those fed on potatoes mixed with a greasy fluid fattened readily, and accumulated much more fat than was contained in the food.

The apparent discrepancy between these facts may be easily explained, when we recollect that, in order that an animal become fattened, it must be supplied not only with the materials of the fat itself, but also with everything else necessary to maintain the body in a healthy condition. Oleaginous matter is one of these necessary substances. The fats taken in with the food are not simply introduced into the body and deposited unchanged. On the contrary, they are altered and used up in the process of digestion and nutrition; while the fats which appear as constituents of the tissues are, in great part, of new formation, and are produced from materials derived, perhaps, from a variety of sources.

It is certain, then, that either one or the other of these two groups of substances, saccharine or oleaginous, must enter into the composition of the food; and furthermore, that, though oily matter may sometimes be produced in the body from the sugars, it is also necessary for perfect nutrition that fat be supplied, under its own form, with the food. For

[1] Annales de Chimie et de Physique, 3d series, tome xiv. p. 400.

man it is natural to have them both associated in the alimentary materials. They occur together in most vegetable substances, and there is a natural desire for them both, as elements of the food.

They are not, however, when alone, or even associated with each other, sufficient for the nutrition of the animal body. Magendie found that dogs, fed exclusively on starch or sugar, perished after a short time with symptoms of profound disturbance of the nutritive functions. An exclusive diet of butter or lard had a similar effect. The animal became exceedingly debilitated, though without much emaciation; and after death, all the internal organs and tissues were found infiltrated with oil. Boussingault[1] performed a similar experiment, with a like result, upon a duck, which was kept upon an exclusive regimen of butter. "The duck received 90 to 100 grammes of butter every day. At the end of three weeks it died of *inanition.* The butter oozed from every part of its body. The feathers looked as though they had been steeped in melted butter, and the body exhaled an unwholesome odor like that of butyric acid."

Lehmann was led to the same result by experiments performed upon himself for the purpose of ascertaining the effect produced on the urine by different kinds of food.[2] This observer confined himself first to a purely animal diet for three weeks, afterward to a purely vegetable one for sixteen days, without any marked inconvenience. He then put himself upon a regimen consisting entirely of non-nitrogenous substances, starch, sugar, gum, and oil, but was only able to continue this diet for two, or at most for three days, owing to the disturbance of the general health which supervened. The unpleasant symptoms, however, immediately disappeared on his return to an ordinary mixed diet. In some instances a restricted diet of this kind can be borne for a longer time. Dr. Parkes[3] kept two soldiers upon non-nitrogenous food alone for five consecutive days without their exhibiting serious signs of physical exhaustion. Prof. Wm. A. Hammond,[4] in experiments performed upon himself, was enabled to live for ten days on a diet of boiled starch and water. After the third day, however, the general health began to deteriorate, and became much disturbed before the termination of the experiment. The prominent symptoms were debility, headache, pyrosis, and palpitation. After the starchy diet was abandoned, it required some days to restore the health to its usual condition.

Nitrogenous Ingredients of the Food.

The nitrogenous or albuminous nutritive principles enter so largely into the constitution of the animal tissues and fluids, that their importance, as elements of the food, is easily understood. No food can be

[1] Chimie Agricole. Paris, 1854, p. 166.

[2] Journal für praktische Chemie, Band xxvii. p. 257.

[3] Proceedings of the Royal Society of London, March 2d, 1871.

[4] Experimental Researches, being the Prize Essay of the American Medical Association for 1857.

long nutritious, unless a certain proportion of these substances be present in it. Since they are so abundant as ingredients of the body, their absence from the food is felt more speedily than that of any other substance except water. They have, therefore, sometimes received the name of "nutritious substances," in contradistinction to those of the second class, which contain no nitrogen, and which are found to be insufficient for the support of life. The albuminous substances, however, when taken alone, are no more capable of supporting life indefinitely than the others. It was found in the experiments of the French "Gelatine Commission"[1] that animals fed on pure fibrine and albumen, as well as those fed on gelatine, become, after a short time, much enfeebled, refuse the food offered to them, or take it with reluctance, and finally die of inanition. This result has been explained by supposing that these substances, when taken alone, excite after a time such disgust that they are either no longer taken, or if taken are not digested. But this disgust is simply an indication that the substances used are insufficient and finally useless as articles of food, and that the system demands other materials for its nourishment. It is well described by Magendie, in the report of the commission above alluded to, while detailing his investigations on the nutritive qualities of gelatine. "The result," he says, "of these first trials was that pure gelatine was not to the taste of the dogs experimented on. Some of them suffered the pangs of hunger with the gelatine within their reach, and would not touch it; others tasted of it, but would not eat; others still devoured a certain quantity once or twice, and then obstinately refused to make any further use of it."

In one instance, Magendie succeeded in inducing a dog to take a considerable quantity of pure fibrine daily throughout the whole course of the experiment; but notwithstanding this, the animal became emaciated, and died at last with the symptoms of inanition.

It is evident, therefore, that no single proximate principle, nor even any one class alone, can be sufficient for nutrition. The albuminous substances are first in importance because they constitute the largest part of the mass of the body; and exhaustion follows more rapidly when they are withheld than when the animal is deprived of other kinds of alimentary matter. But starchy and oleaginous substances are also requisite; and the body feels the want of them sooner or later, though it may be plentifully supplied with albuminous food. Finally, the inorganic saline matters, though in smaller quantity, are also necessary to the continued maintenance of life. In order that the animal tissues and fluids remain healthy, and take their proper part in the functions of life, they must be supplied with all the ingredients necessary to their constitution; and a man may be starved to death at last by depriving him of sodium chloride or lime phosphate as surely, though not so rapidly, as if he were deprived of albumen or oil.

[1] Comptes Rendus de l'Académie des Sciences. Paris, 1841, tom. xiii. p. 267.

Composition of Different Articles of Food.

In the most valuable and nutritious kinds of food, which have been adopted by the universal and instinctive choice of man, the first three classes of proximate principles are all more or less abundantly represented. In all there exists naturally a certain proportion of saline matter; and water and sodium chloride are generally taken in addition.

Milk.—In milk, the first food supplied to the infant, and largely employed in various culinary preparations, all the important groups of nutritive substances are present. It is a white, opaque fluid, consisting, 1st, of a serous portion, which contains albuminous matters, sugar, and mineral salts in solution, and, 2d, of fatty globules suspended in the watery liquid. It is this mixture of oleaginous particles with a serous fluid which gives to the milk its opacity and its white color. Its richness in fatty matter may therefore be estimated from these physical qualities. The ingredients in cow's milk are present in the following proportions, according to Payen:

Composition of Cow's Milk in 1000 parts.

Water	864
Nitrogenous matter (caseine and albumen)	43
Sugar of milk	52
Fat	37
Mineral salts	4
	1000

Cow's milk resembles human milk in its general characters, but contains a larger proportion of solid ingredients, especially of the nitrogenous and saccharine matters, fat being present in nearly the same amount in each. Sheep and goat's milk is richer in both nitrogenous and fatty matters; while the milk of the ass and the mare contains a greater abundance of sugar, but is comparatively poor in nitrogenous matter and fat. The nitrogenous matter of milk consists almost entirely of caseine, associated with a very small proportion of albumen. Owing to the relative quantity of these two substances, milk does not solidify on boiling, but merely covers itself with a thin pellicle of coagulated albumen, the caseine remaining liquid. The addition of any acid, however, such as acetic or tartaric acid, will precipitate the caseine and curdle the milk. If milk be allowed to remain exposed to the air at a moderately warm temperature, it curdles spontaneously, owing to the development of lactic acid, due to a transformation of its sugar; and the same change will sometimes occur instantaneously from electric disturbance, during a thunder storm.

The caseine of milk, artificially coagulated by the action of rennet, constitutes *cheese.* Rennet is the dried contents and mucous membrane of the stomach of the calf, the animal being killed and the stomach taken out while digestion is in full activity and the gastric fluids abundantly secreted. A faintly acidulated infusion of this substance even in small quantity, added to fresh milk at the temperature of 30° (86° F.)

produces complete coagulation in fifteen or twenty minutes. The coagulum is drained from the watery serum or "whey," and afterward pressed into the form of cheese. The variety in consistency and flavor of different cheeses depends mainly on the proportion of fatty matter retained in the coagulum, and upon certain slow changes, in the nature of fermentations, which go on in it subsequently.

The fatty matter of milk is suspended in the serous portion under the form of minute spheroidal masses. These little masses or "milk-globules" are not quite fluid at ordinary temperatures, but have a semi-solid consistency owing to their containing a considerable proportion of palmitine. The fat globules, separated by churning from the other ingredients of the milk, and made to unite into a coherent mass, constitute *butter*. This substance, accordingly, represents simply the oleaginous ingredients of the milk; and when purified from the watery portions entangled with it, consists mainly of palmitine and oleine, together with a small proportion of peculiar odoriferous and flavoring ingredients, the principal of which has received the name of "butyrine." These substances are usually mingled in the following proportions:

Palmitine	68 parts.
Oleine	30 "
Butyrine and other flavoring matters	2 "
	100

When well prepared and in good condition, butter constitutes one of the most valuable and easily assimilated forms of oleaginous food. If contaminated with the remains of the nitrogenous matter of the milk, its fatty ingredients after a time become decomposed with the development of volatile fatty acids; in which condition the butter is said to be "rancid," and is no longer fit for food.

Bread.—The cereal grains resemble each other more or less in their constitution, all of them containing starch, nitrogenous matter, dextrine or sugar, fat, and mineral salts in various proportions. Wheat is distinguished from the remainder in containing a considerably larger quantity of nitrogenous matter as compared with the other ingredients, and in the peculiarly adhesive or fibrinous quality of this substance, which has received accordingly the name of "gluten." The different grains in common use for food have when dry the following average composition, according to Payen.

Composition of the Cereal Grains.

	Nitrogenous matter.	Starch.	Dextrine, etc.	Fat.	Cellulose.	Mineral salts.
Wheat	18.00	66.80	7.50	2.10	3.10	2.50
Rye	12.50	64.65	14.90	2.25	3.10	2.60
Barley	12.96	66.43	10.00	2.76	4.75	3.10
Oats	14.39	60.59	9.25	5.50	7.06	3.25
Indian corn . .	12.50	67.55	4.00	8.80	5.90	1.25
Rice	7.55	88.65	1.00	0.80	1.10	0.90

Thus, of the different grains, that of oats contains, next to wheat, the largest proportion of nitrogenous matters; but it also contains a considerable abundance of cellulose, or indigestible vegetable tissue, which interferes with its nutritive quality as human food. Indian corn is especially rich in fatty ingredients, while rice consists mainly of starch, and is the poorest of all in both nitrogenous and fatty ingredients.

Wheat is more valuable than the other cereal grains for the purpose of making bread, not only on account of its larger proportion of albuminous matter, but also on account of the peculiar glutinous quality of this ingredient, already mentioned.

In preparing the wheat, the grains are first cleansed from husks and adherent foreign material, ground into meal, and the finer and whiter portions derived from the interior of the grain separated by sifting and bolting from the coarser external parts, or bran. Thus purified, the flour consists of starch, gluten, diastase, dextrine, a little fat, sometimes a trace of sugar, mineral salts, and about 15 per cent. of water, which is never fully expelled by ordinary drying. For making into bread, the flour is mixed with about one-half its weight of water, and kneaded into a flexible dough of uniform consistency. The next process is the fermentation of the dough. For this purpose a little yeast is incorporated with it, and the mixture allowed to remain for a few hours at a temperature of about 25° (77° F.). During this time the sugar originally present in the flour, and that produced from the starch and dextrine by the action of the diastase, passes into fermentation under the influence of the yeast, and is transformed into alcohol and carbonic acid. The alcohol is dissipated by evaporation; but the carbonic acid, which is generated in small gas-bubbles, is entangled by the tenacious gluten of the flour, and the dough is thus puffed up into a spongy, reticulated mass. When the fermentation of the dough is completed, it is placed in ovens, and baked at a temperature of 210° (about 400° F.). The effect of this heat is to cook the glutinous part of the dough, communicating to it an agreeable flavor, and at the same time solidifying it; so that the substance of the baked loaf, when cut open, retains its spongy and reticulated texture. It is thus made easy of mastication, and readily permeable by the saliva and other digestive fluids. The spongy texture acquired by bread is the main object of its fermentation, although an agreeable flavor is also developed by the process, which does not exist in unfermented bread. The interior of the loaf, in baking, does not rise above 100° (212° F.); the exterior, which is subjected to a higher temperature, becomes covered with a crust formed of partially torrefied starch or dextrine, and caramelized sugar. The interior of the loaf also usually retains a little glucose, which is not all destroyed in the process of fermentation. A considerable portion of the water which was mixed with the flour remains permanently united with its organic ingredients; so that 100 parts of flour will usually yield, after baking, 130 parts, by weight, of bread.

Wheaten bread, prepared in this way, has the following average composition:

COMPOSITION OF WHEATEN BREAD.

Starchy matters (starch, dextrine, glucose)	56.7
Albuminous matter (gluten, etc.)	7.0
Fatty matter	1.3
Mineral matter (calcareous, magnesian, and alkaline salts)	1.0
Water	34.0
	100.0

Thus, while bread contains an abundance of albuminous and starchy matter, it is deficient in fat; and instinct accordingy leads us to take with it butter, fat bacon, or some other form of oleaginous food.

The good quality of bread, aside from that of the flour of which it is made, depends mainly on the success of the process of fermentation. If this be incomplete, the bread is heavy, and not sufficiently reticulated in texture. If it be allowed to go on beyond the proper time, it passes into an acid fermentation, and develops a sour taste. If properly conducted, the bread is uniformly light and spongy, and has no acid reaction.

Meat.—The muscular flesh of various animals affords an exceedingly valuable and nutritious food, of which beef, mutton, and venison hold the highest place. The muscular fibre itself consists almost exclusively of nitrogenous matters, but in point of fact the flesh used for food is always accompanied with more or less adipose tissue, and even when freed from visible fat, there is always, according to Payen and Pavy, more or less oleaginous matter entangled with the muscular fibres. In various kinds of meat, and even in meat from different parts of the same animal, the proportion of fat will vary considerably; but it was found by Pavy, in one of the best and most commonly used portions of beef, to amount to about 5 per cent. of the whole.

COMPOSITION OF BEEF FLESH.

Water	77.5
Albuminous matter	16.0
Fat	5.0
Mineral salts	1.5
	100.0

The mineral matters consist of alkaline chlorides and phosphates, with phosphates of lime and magnesia.

In the cooking of meat by roasting or broiling, the external parts are exposed to a rapid heat of 120° or 130° (260° F.) by which their albuminous parts are coagulated, their coloring matter turned brown, and a characteristic flavor developed. The interior, which does not rise above 65° (150° F.) remains red and juicy, its fluids being protected from evaporation by the coagulation of the outer portions. In boiling, where the meat is cooked by contact with the boiling water, none of it rises

above the temperature of 100° (212° F.); but this may penetrate throughout the whole substance of the meat, producing a uniform decolorization. Notwithstanding the coagulation of the albuminous liquids by boiling, the fibrous connective tissues are gelatinized, and the muscular flesh thus partially softened and disintegrated. On the whole, the effect of cooking upon meat is to increase the consistency of its albuminous ingredients, its principal benefit being the attractive flavor which is developed by the aid of heat, and no doubt an increased digestibility from the same cause. By either method, meat loses in cooking from 25 to 30 per cent. of its weight, principally by the escape of water and liquefied fat.

Eggs.—The eggs of various animals are used for food, as those of the common fowl, the duck, goose, turkey, seafowl, turtles, and the roe of many kinds of fish. Those of the common fowl, which are the most abundantly used, may be considered as representing the general qualities of this article of nourishment. They consist of the globular "yolk," surrounded by a layer of albumen or "white." The composition of these two portions is nearly the same, excepting that the yolk contains a larger proportion of solids and particularly of fatty matter which gives to it its yellow color and rich flavor. A comparative analysis of the yolk and white is as follows:

Composition of the Fowl's Egg.

	Yolk.	White.
Albuminous matter	16.0	20.4
Fat	30.7	
Mineral salts	1.3	1.6
Water	52.0	78.0
	100.0	100.0

The mineral matters consist mainly of the sodium and potassium chlorides, potassium sulphate, and lime and magnesium phosphates. Of the entire contents of the egg, exclusive of the shell, the yolk constitutes one-third, and the white two-thirds. Cooking produces but little effect upon eggs except to coagulate their albuminous matters, since these are comparatively but little susceptible of developing any marked flavor by the action of heat.

Vegetables.—Of the different vegetables used as food, some are valuable for their solid starchy and albuminous ingredients, others mainly for their saccharine and watery juices. The former are nutritious in the ordinary sense of the word, though much less so than bread or animal food; the latter are useful for supplying certain materials contained in the fresh vegetable juices which are essential to the continued maintenance of health. The most important of the first group are represented by the potato and the leguminous seeds. The tuber of the potato abounds in starch, but is poor in other nutritive ingredients.

Composition of the Potato.

Starch	20.0
Albuminous matter	2.5
Sugar and gum	1.1
Fatty matter	0.1
Cellulose	1.0
Mineral and vegetable salts	1.3
Water	74.0
	100.0

The leguminous seeds, on the other hand, contain an abundance of albuminous matter, similar in character to the caseine of milk, and called "legumine."

Composition of White Beans.

Starch	55.7
Albuminous matter	25.5
Fatty matter	2.8
Cellulose	2.9
Mineral salts	3.2
Water	9.9
	100.0

The composition of dried peas is very similar to the above, the starchy matters only being present in rather larger, the albuminous ingredients in rather smaller proportion. Notwithstanding the abundance of nitrogenous matter in leguminous seeds, its quality is inferior to that contained in the cereal grains. Peas and beans also have a texture which renders them comparatively difficult of digestion, and requires long boiling to fit them for use as food. The same is true of many juicy and saccharine roots, such as beets and parsnips, which appear to have a comparatively soft consistency, but which nevertheless need prolonged boiling. The object and effect of the cooking process in vegetables generally is to disintegrate and soften their texture, and particularly, by the aid of heat and moisture, to bring their starchy ingredients into the hydrated condition. Raw starch is nearly or quite indigestible by man, and if taken into the stomach under that form will often pass unchanged from the bowels; but when thoroughly hydrated it is easily acted on and transformed into glucose by the digestive fluids. It is for this reason that starchy vegetables require more thorough cooking to render them digestible than most kinds of animal food.

Beside the more solid kinds of vegetable food, many of the pulpy and succulent fruits and herbaceous substances are valuable as an addition to the nutritive regimen—celery, lettuce, parsley, spinach, with all the sweet fruits and melons, are used with advantage either in the raw or cooked form. They introduce into the system a large number of salts of the vegetable acids, such as malates, tartrates, and citrates, the privation of which for a long time is one of the inducing causes of

scurvy. The green parts of vegetables are no doubt also useful by furnishing to the system a supply of iron contained in their chlorophylle.

From what has been said above, it will be seen that the nutritious character of any substance, or its value as an article of food, does not depend simply upon its containing either one of the alimentary substances in large quantity; but upon its containing them mingled together in such proportion as is requisite for the healthy nutrition of the body. What these proportions are cannot be determined from simple chemical analysis, nor from any other data than those derived from observation and experiment.

Requisite Quantity of Food and of its Different Ingredients.

The entire quantity of food required per day varies with the circumstances of the individual, such as the size and weight of the body, the comparative development of the muscular and other systems, the temperature, and especially the amount of physical activity. More food is required, on the average, in cold than in warm weather, more by persons of a muscular than by those of an adipose or phlegmatic constitution, more in a condition of active exertion than in one of comparative repose. Even the proportion of different classes of proximate principles required for nutrition varies to a considerable extent according to special conditions. When the individual is in a perfectly healthy condition, and so situated that he can supply himself at will with any kind of nourishment desired, the natural demands of the appetite afford the surest criterion for both the quantity and quality of the food to be used. But not infrequently provision must be made in advance for supplies destined to last over a considerable period, as in the case of military or exploring expeditions, or for the inmates of hospitals or asylums where the diet must be regulated to a great extent upon a uniform plan. It therefore becomes important to know both the quantity and kind of food necessary for the support of life.

The standard adopted for this estimate is that of a healthy adult man, employed in active but not exhausting occupation. The amount requisite will be found to vary in either direction from this standard, according to the circumstances above mentioned. The average requirements as given by different authors do not vary materially from each other in any essential particular. According to our own observations, a man in full health, taking active exercise in the open air, and restricted to a diet of bread, fresh meat, and butter, with water and coffee for drink, consumes the following quantities per day:

Quantity of Food required per day.

Meat	453	grammes.
Bread	540	"
Butter or fat	100	"
Water	1530	"

This represents the requisite daily quantity of food and the proportions of its different kinds, when composed of such articles as are most

completely nutritious, and of the most uniform composition. For the continued maintenance of health and strength in a working condition, other articles, such as fresh vegetables, sugar, milk, fruit, etc., should be mingled with the above, in a variety of proportions; but there is no doubt that bread and fresh meat, with a certain quantity of fat, will prove sufficient for the wants of the system, for a longer time than any other single articles of food.

Such a diet also affords the best means of ascertaining the absolute and relative quantities of the different proximate principles required for food. If we take the average composition of meat and bread, and estimate the quantities of their solid albuminous, starchy, and saline ingredients, together with the water contained in both solid and liquid food, we find that the daily ration is composed nearly as follows:

Albuminous matter	130	grammes.
Starch and sugar	300	"
Fat	100	"
Mineral salts	20	"
Water	2000	"

Of the mineral salts, nearly eight grammes are naturally contained in the substances used for food and drink; the remainder consists of sodium chloride, artificially added to the food, or used in its preparation.

The proportion in which the *albuminous* and the *non-nitrogenous* principles should be mingled in the food is of considerable importance, and this proportion has been determined within very accurate limits. In making such an estimate it is necessary to include the carbohydrates (starch and sugar) and the fats under the same head; but the fats are properly regarded by all writers as having a different alimentary value from the carbohydrates. This depends upon the well-known fact that the final result of the transformation in the living body of all the non-nitrogenous substances is carbonic acid and water, thus representing a process of oxidation, the necessary oxygen being introduced with the inspired air. But the capacity for oxidation of the fats is greater than that of the carbohydrates, as shown by the relative proportion by weight of their constituent elements.

$$\text{The composition, by weight, of starch } (C_6H_{10}O_5) \text{ is } \left\{\begin{array}{ll} C & 72 \\ H & 10 \\ O & 80 \\ \hline & 162 \end{array}\right. \quad \text{or, in 100 parts,} \quad \begin{array}{ll} C & 44.47 \\ H & 6.17 \\ O & 49.36 \\ \hline & 100.00 \end{array}$$

Here the oxygen is already present in sufficient proportion to saturate all the hydrogen by the formation of water; while the 44.47 parts of carbon will unite with 118.58 parts of oxygen to form carbonic acid.

On the other hand, if we take palmitine as representing the average constitution of the fats, we have—

$$\text{The composition, by weight, of fat } (C_{51}H_{98}O_6) \text{ is } \left\{\begin{array}{ll} C & 612 \\ H & 98 \\ O & 96 \\ \hline & 806 \end{array}\right. \quad \text{or, in 100 parts,} \quad \begin{array}{ll} C & 75.93 \\ H & 12.15 \\ O & 11.92 \\ \hline & 100.00 \end{array}$$

Here the oxygen is present in much diminished proportion; and, for complete oxidation of the fat, to form carbonic acid and water, the 75.93 parts of carbon will require 202.48 parts of oxygen, and the 12.15 parts of hydrogen will need 85.28 additional, over and above the 11.92 parts of oxygen already present. Thus the quantities of oxygen appropriated during complete oxidation, by starch and fat respectively, are as follows:

QUANTITY OF OXYGEN REQUIRED FOR THE COMPLETE OXIDATION OF

100 parts of starch	118.58
" " " fat	287.76

A fatty substance, therefore, has a capacity for the production of carbonic acid and water, by oxidation, about 2.4 times greater than that of starch. In estimating, accordingly, the requisite quantity of all the non-nitrogenous matters taken together, the fat is calculated as starch upon this basis; one part of fat, by weight, being reckoned as equal to 2.4 parts of starch. This quantity, added to that of the carbohydrates in the food, is sometimes called the "starch-equivalent" of the non-nitrogenous matters.

If we ascertain the amount of solid albuminous and non-nitrogenous matter contained in the daily food of an ordinary nutritious diet of mixed quality, we find that the non-nitrogenous matters, reckoned as starch, amount to four or five times as much as the albuminous ingredients. A comparison of our own observations with the estimates and diet tables of Moleschott, Payen, and Playfair, all of which correspond in the main with each other, gives the following as the average daily quantity of these two classes of proximate principles in the food.

Albuminous matter	130 grammes.
Non-nitrogenous matter, as starch	600 "

Thus albuminous matter constitutes rather less than one-fifth of the entire food, for a healthy adult in active occupation; and its quantity is to that of the non-nitrogenous matters as 1 to 4.62.

This proportion varies to some extent with the age and condition of the individual. In human milk, which at first forms the exclusive food of the young infant, according to the average analyses of Simon, Vernois, and Becquerel, as given by Milne Edwards, the albuminous ingredients are to the non-nitrogenous matters reckoned as carbohydrates in the proportion of 1 to 2.95. In cow's milk, upon which the young calf is sustained, the proportion is as 1 to 3.27; while in green grass and hay, upon which the adult animal feeds, it is as 1 to 11.70 and 1 to 9.28 respectively. The larger proportion of albuminous matter in the food at this early age is evidently connected with the growth which is then taking place. As the nitrogenous principles constitute much the larger part of the solid organic matters contained in the body, the steady increase in weight during the growing period demands a corresponding supply of these substances in the food.

There is also evidence that the requisite proportion of nitrogenous

principles varies in the adult with the amount of physical activity. A condition of bare subsistence may be maintained upon a diet in which the albuminous substances are in smaller, and the non-nitrogenous matters in larger proportion; but when the system is habitually called upon for a greater amount of muscular exertion, the proportion of albuminous matters in the food must be increased. This is a well-known fact in regard to horses and working cattle generally. In a state of comparative inactivity they may be supported mainly upon grass or hay, in which the proportion of nitrogenous to non-nitrogenous matter is not more than 1 to 9.28; but when employed in active labor they require a liberal supply of oats, in which the proportion is as 1 to 7.13. In Dr. Playfair's diet tables, which were collected with great care from a variety of sources, including those of prisons and infirmaries, those of the American and European armies during peace and in active service, and of certain hard-working laborers, the increase of albuminous matter with increased labor is a marked feature. While in a bare subsistence diet the proportion of albuminous to non-nitrogenous matter is as 1 to 5.87, in that of active laborers it is as 1 to 4.34. The following table will show the relative increase of the two kinds of food under different conditions of exercise, as calculated from Dr. Playfair's data.

Relative Increase, under Different Conditions, of Albuminous and Non-Nitrogenous Matters in the Food.

	Albuminous matter.	Non-nitrogenous matter.
Bare subsistence diet	100	100
Full diet with moderate exercise . .	180	161
Diet of active laborer	232	171
Diet of hard-worked laborer . . .	242	189

As these diet tables were adopted by the various civil and military authorities as the result of long experience in the practical adaptation of food to the amount of work performed, they may be regarded as expressing with great approximation to certainty the physiological requirements under different conditions. They are corroborated by the variation in diet adopted in the convict establishments of Great Britain, as given by Pavy.[1] In the change from "Light-labor Diet" to "Hard-labor Diet," while the non-nitrogenous food is increased only 13.37 per cent., the albuminous food is increased 16.15 per cent.

It is evident, therefore, that increased physical exertion requires a greater proportional increase in the albuminous than in the non-nitrogenous ingredients of the food.

It is also a matter of interest to determine the quantity, source, and destination of the different *chemical elements* entering into the composition of the food. Taking the average chemical composition of albuminous matters and fat, and that of the carbohydrates, we find that a man under ordinary full diet takes into his system daily the constituents of the food, in round numbers, as follows:

[1] On Food and Dietetics. Philadelphia edition, 1874, p. 433.

Daily Consumption in the Food.

				C	H	O	N	S
Albuminous matter,	130 grammes,	containing		70	10	29	20	1
Starch . .	300	"	"	134	18	144		
Fat . . .	100	"	"	76	12	12		
				280	40	185		

Of these elementary bodies, carbon and nitrogen are considered especially important as constituents of the food, carbon as forming the most abundant and characteristic ingredient of all organic combinations, and nitrogen, as the distinguishing element of albuminous substances. Of these two, accordingly, the system requires daily, to be supported in an active condition, about 20 grammes of nitrogen and about 280 grammes of carbon. This fact alone makes it evident that a mixed diet of animal and vegetable food is the most available for man. Meat contains, according to the analyses of Payen, 3 per cent. of nitrogen and 11 per cent. of carbon. Consequently, if the diet were composed exclusively of this food, the necessary quantity of nitrogen would be supplied by 666 grammes of meat; but in order to obtain the required carbon, 2545 grammes would need to be consumed, thus involving a great waste of its nitrogenous matter. On the other hand, bread, the most nutritious of all vegetable substances, contains only 1 per cent. of nitrogen and 30 per cent. of carbon. Therefore, if this were the only food used, 933 grammes would be sufficient to supply all the carbon; but, in order to obtain the due amount of nitrogen, it would be necessary to consume 2000 grammes. A mixture, accordingly, of the two kinds of food, in which nitrogenous and hydrocarbonaceous matters respectively preponderate, is best adapted to supply the wants of the system without unnecessary expenditure of material.

The changes undergone in the body, and the final destination of the ingredients of the food, vary for different kinds. The carbohydrates no doubt, after serving the purposes for which they are intended in the animal economy, are finally expelled under the form of carbonic acid and water. The action of the oxygen, introduced with the inspired air, produces this result by uniting with the carbon of the organic body, while its own hydrogen and oxygen, already present in the relative quantities to produce water, are liberated under that form. This result is expressed by the following formula:

$$\underset{\text{Starch.}}{C_6H_{10}O_5} + O_{12} = \underset{\text{Carbonic acid.}}{C_6O_{12}} + \underset{\text{Water.}}{H_{10}O_5}.$$

Thus the change undergone by starch and allied substances in the animal body, where they are consumed, is precisely the reverse of that taking place in plants during the act of vegetation, by which they are produced.

For the fats the change is a similar one, their only final products, so far as we know, being carbonic acid and water. In this process, however, the fats require, as already mentioned, a greater supply of extra-

neous oxygen, since, beside their larger proportion of carbon, they also contain hydrogen which requires further oxidation, in order to form water. The change thus undergone by fatty substances may be expressed as follows:

$$\underset{\text{Fat.}}{C_{51}H_{98}O_6} + O_{145} = \underset{\text{Carbonic acid.}}{C_{51}O_{102}} + \underset{\text{Water.}}{H_{98}O_{49}}.$$

In the case of the albuminous matters the process is a different one. These substances contain an element, namely, nitrogen, which does not appear in the carbonic acid and watery vapor of the expired breath, but forms a distinguishing constituent of the crystallizable matters of the urine. Of these matters, urea is by far the most abundant, and, as already mentioned, fully five-sixths of the nitrogen taken in with the food reappears as an ingredient of urea, while the remainder is included in the creatinine and uric and hippuric acids of the urine, and in the excrementitious substance of the feces.

There is evidence, however, that the nitrogenous matters also take part in the formation of carbonic acid; that is, although all their nitrogen is discharged under the form of urea and other similar combinations in the urine and feces, all their carbon does not appear in these excretions, and must pass out by some other channel. While, as we have seen, 130 grammes of albuminous matter are taken daily with the food, containing 70 grammes of carbon, only 35 grammes of urea are discharged during the same time, containing 7 grammes of carbon; and, according to the most accurate analyses,[1] not more than 23 grammes are discharged daily by both the urine and feces together. This leaves unaccounted for about 47 grammes of carbon, or two-thirds of the original quantity, which must pass out from the body under some other form of combination. The same thing is true, to a considerable extent, of the hydrogen of these substances, of which 10 grammes are introduced daily as an ingredient of the albuminous matters of the food, while not more than 5 or 6 grammes are discharged in organic combinations with the urine and feces. The albuminous matters, therefore, not only give rise to the elimination of urea, but also contribute to the production of carbonic acid and water.

The manner in which this takes place is probably by the separation of some of the elements of albumen combined as urea, after which the remainder are left behind as a non-nitrogenous substance. If we adopt, for the constitution of an albuminous body, exclusive of its sulphur, the formula $C_{72}H_{112}N_{18}O_{23}$, and take away from it all the nitrogen in the form of urea, a substance will remain analogous in composition to a fat, thus—

Albumen	C_{72}	H_{112}	N_{18}	O_{23}
9 Urea (CH_4N_2O)	C_9	H_{36}	N_{18}	O_9
	C_{63}	H_{76}		O_{14}

[1] Ranke, Grundzüge der Physiologie des Menschen. Leipzig, 1872, p. 298.

The remaining substance may then undergo complete oxidation without the further production of any nitrogenous compound. This double result of the decomposition of the albuminous substances, together with the fact that we take habitually between four and five times as much non-nitrogenous as nitrogenous matter in the food, will explain the great preponderance in quantity of carbonic acid as an excretion over urea. For while the average daily quantity of urea discharged is only 35 grammes, the carbonic acid exhaled with the breath amounts to from 700 to 800 grammes per day; the entire quantity of the carbonic acid produced being, by weight, fully twenty times as great as that of the urea. Urea is a nitrogenous substance separated by decomposition from the albuminous ingredients of the system; while carbonic acid represents the combination of its remaining elements with the abundant oxygen introduced by the breath.

The quantities of the various substances taken in with the food and discharged with the excretions are liable to many variations from the changing condition of the individual. If the body be increasing in weight, the substances introduced will be greater in quantity than those discharged; if it be diminishing, the material discharged will be more than that introduced. Even in the healthy adult, where the body does not sensibly gain or lose weight for long intervals, observation has shown that there are frequent fluctuations of small extent, and that the income for any single day rarely counterbalances exactly the outgo for the same period. Consequently the quantities given in the preceding tables cannot be taken as furnishing, in any case, a uniform and invariable standard, but only as showing what, upon the whole, are the relative proportions of the different ingredients entering into the composition of the food and of the bodily frame. And although for many of them we are not yet able to ascertain their quantities with sufficient accuracy for determining all the changes which they undergo in the system, yet there is no doubt of the main result produced by the internal transformation of the ingredients of the food. We have certain nutritious substances introduced on the one hand, and certain excrementitious products discharged on the other, which may be expressed as follows:

Introduced with the Food.	Discharged with the Excretions.
Albuminous matter.	Urea.
Fat.	Carbonic acid.
Carbohydrates.	Water.

This represents the decomposition and metamorphosis of the organic substances proper; while the mineral ingredients of the food, as a rule, pass through the system unchanged.

CHAPTER VIII.

DIGESTION.

Digestion is the process by which the food is reduced to a form in which it can be absorbed from the intestinal canal, and taken up by the bloodvessels. This process does not occur in vegetables, which are dependent for their nutrition upon materials which are supplied to them in a form already fitted for absorption.

Carbonic acid, ammonium carbonate, and ammonium nitrate exist in a gaseous form in the atmosphere, or are brought down in solution by the rain, and penetrate the soil to the roots of the growing plants; while many of the mineral salts, as sulphates, nitrates, and carbonates, are also present in the soil in a soluble condition. Thus they require no alteration before being taken up by the tissues of the plant. The only known exception to this is in the case of materials composed of the earthy carbonates and phosphates, which are insoluble or nearly so in water, but which are known to be corroded and rendered soluble by the acid juices of the plant-roots in contact with them. As a general rule, the substances requisite for vegetation are directly absorbed from the exterior in their original condition. But with animals and man the case is different. They cannot subsist upon inorganic substances only, but require for their support materials which have already been organized, and which have previously constituted a part of animal or vegetable bodies. Their food is almost invariably solid or semi-solid when taken, and insoluble in water. Meat, bread, fruits, vegetables, and the like, are all taken into the stomach in a solid and insoluble condition; and even substances naturally fluid, such as milk, albumen, white of egg, are nearly always, in the human species, more or less solidified by the process of cooking, before being taken into the stomach.

In animals, accordingly, the food requires to undergo a process of digestion or liquefaction, before it can be absorbed. In all cases, the general characters of this process are the same. It consists essentially in the food being received into a canal, running through the body from mouth to anus, called the "alimentary canal," in which it comes in contact with certain digestive fluids, which act upon it in such a way as to liquefy and dissolve it. These fluids are secreted by the mucous membrane of the alimentary canal, and by certain glandular organs situated in its neighborhood. The food consists, as we have seen, of a mixture of various substances, having different physical and chemical properties; and the several digestive fluids are also different from each other, each

one of them exerting a peculiar action, which is more or less confined to particular species of food. As the food passes through the alimentary canal from above downward, those parts of it which become liquefied are successively removed by absorption, and taken up by the vessels; while the remaining portions, consisting of the indigestible matter, together with the refuse of the intestinal secretions, gradually acquire a firmer consistency owing to the absorption of the fluids, and are finally discharged from the intestine under the form of feces.

Fig. 26.

ALIMENTARY CANAL OF FOWL.—*a.* Œsophagus. *b.* Crop. *c.* Proventriculus, or secreting stomach. *d.* Gizzard, or triturating stomach. *e.* Intestine. *f.* Two long cæcal tubes which open into the intestine a short distance above its termination.

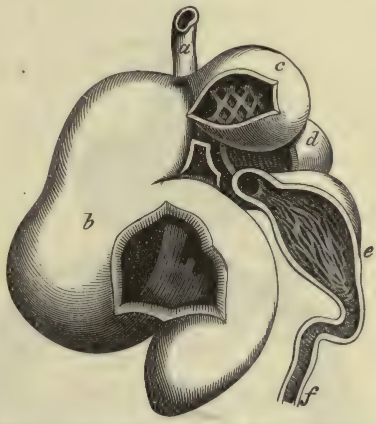
In different species of animals, the difference in their habits, in the constitution of their tissues, and in the character of their food, is accompanied with a corresponding variation in the anatomy of the digestive apparatus, and the character of the secreted fluids. As a general rule, the digestive apparatus of herbivorous animals is more complex than that of the carnivora; since, in vegetable substances, the nutritious matters are often present in a comparatively solid and unmanageable form, as, for example, in raw starch and the cereal grains, and are nearly always entangled among vegetable cells and fibres of an indigestible character. In those instances where the nutriment consists mostly of grass, leaves, twigs, and roots, the digestible matters bear only a small proportion to the entire quantity; and a large mass of food must therefore be taken, in order that the requisite amount of nutritious material may be extracted from it. In such cases, accordingly, the alimentary canal is large and long; and is divided into many compartments, in which different processes of disintegration, transformation, and solution are carried on.

In the common fowl, for instance (Fig. 26), the food, consisting mostly of grains, or of insects with hard, coriaceous integument, first passes down the œsophagus (*a*) into a diverticulum or pouch (*b*) termed the crop. Here it remains for a time mingled with a watery secretion in which the grains are macerated and softened. The food is then carried farther down until it reaches a second dilatation (*c*), the proventriculus, or secreting stomach. The mucous membrane here is thick and glandular, and is provided with numerous secreting follicles. From them an acid fluid is poured out, by which the food is subjected to further changes. It next passes into the gizzard (*d*), or triturating

stomach, a cavity inclosed by thick muscular walls, and lined with a tough and horny epithelium. Here it is subjected to the crushing and grinding action of the muscular parietes, assisted by grains of sand and gravel, which the fowl instinctively swallows with the food, by which it is so triturated and disintegrated, that it is reduced to a uniform pulp, upon which the digestive fluids can effectually operate. The mass then passes into the intestine (*e*), where it meets with the intestinal juices, which complete the process of solution; and from the intestinal cavity it is finally absorbed in a liquid form, by the vessels of the mucous membrane.

In the ox, the sheep, the camel, the deer, and all ruminating animals, there are four distinct stomachs, each lined with mucous membrane of a different structure, and adapted to perform a different part in the digestive process. (Fig. 27.) The first two, situated side by side at the lower extremity of the œsophagus (*a*), consist of the *rumen* or paunch (*b*), a large sac, itself partially divided by incomplete partitions, and lined by a mucous membrane thickly set with long prominences or villi; and the *reticulum* (*c*) or second stomach, so called from the intersecting folds or ridges of its mucous membrane, which give it a reticulated or honey-combed appearance. Into these two stomachs the food is received when first swallowed by the animal in feeding or browsing, and remains there for some time, especially in the capacious rumen, slowly macerated and softened by the action of the warmth and watery fluids, but not undergoing any marked chemical action. When the animal has finished browsing, and the process of rumination commences, the food is regurgitated into the mouth by an inverted action of the muscular walls of the paunch and œsophagus, and slowly masticated. It then descends again along the œsophagus; but the lateral opening which communicates with the first two stomachs is now closed by muscular action, and the œsophagus, thus converted into a tubular canal, conducts the masticated food into a third stomach, the *omasus* or "psalterium" (*d*), in which the mucous membrane is arranged in thin longitudinal folds, lying parallel with each other, like the leaves of a book, thus increasing considerably its extent of surface. The exit from this cavity leads directly into the *abomasus* or "rennet" (*e*), the true digestive stomach, in which the mucous membrane is soft, thick, and glandular, and in which an acid

Fig. 27.

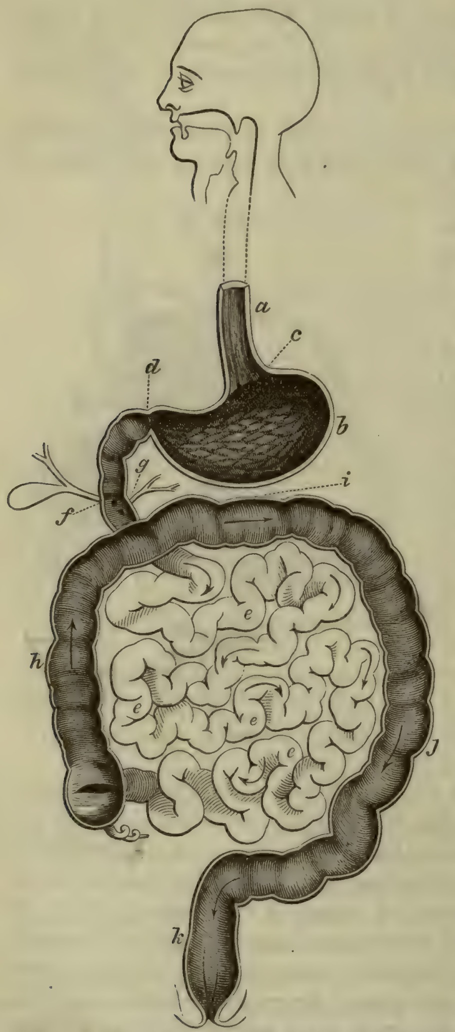


Compound Stomach of Ox.—*a.* Œsophagus. *b.* Rumen, or first stomach. *c.* Reticulum, or second. *d.* Omasus, or third. *e.* Abomasus, or fourth. *f.* Duodenum. (Rymer Jones.)

solvent fluid is secreted. Then follows the intestinal canal with its various divisions and variations.

In the carnivora the alimentary canal is shorter and narrower than in the preceding, and presents fewer complexities. The food upon which these animals subsist is softer than that of the herbivora, and less encumbered with indigestible matter; so that the process of its solution requires a less extensive apparatus.

Fig. 28.



Human Alimentary Canal.—*a.* Œsophagus. *b.* Stomach. *c.* Cardiac orifice. *d.* Pylorus. *e.* Small intestine. *f.* Biliary duct. *g.* Pancreatic duct. *h.* Ascending colon. *i.* Transverse colon. *j.* Descending colon. *k.* Rectum.

In the human species, the food is naturally of a mixed character, containing both animal and vegetable substances. But, notwithstanding this difference in the kind of nourishment, the digestive apparatus in man resembles closely that of the carnivora. For the vegetable matters which we take as food are, in the first place, artificially separated, to a great extent, from indigestible impurities; and secondly, they are so softened by the process of cooking as to become nearly or quite as digestible as animal substances.

In the human species the process of digestion, though simpler than in the herbivora, is still somewhat complex. The alimentary canal is divided into different compartments or cavities, which communicate with each other by narrow orifices. At its commencement (Fig. 28) we find the cavity of the *mouth*, which is guarded at its posterior extremity by the muscular valve of the isthmus of the fauces. Through the pharynx and œsophagus (*a*), it communicates with the second compartment, or the *stomach* (*b*), a flask-shaped dilatation, guarded at its cardiac and pyloric orifices by circular bands of muscular fibres. Then follows

the *small intestine* (*e*), different parts of which, owing to the varying structure of their mucous membrane, have received the different names of duodenum, jejunum, and ileum. In the duodenum are situated the orifices of the *biliary* and *pancreatic* ducts (*f*, *g*). Finally comes the *large intestine* (*h*, *i*, *j*, *k*), separated from the smaller by the ileo-cæcal valve, and terminating, at its lower extremity, by the anus, at which is situated a double sphincter, for the purpose of guarding its orifice. Everywhere the alimentary canal is composed of a mucous membrane and a muscular coat, with a layer of submucous connective tissue between the two. The muscular coat is composed of a double layer of longitudinal and transverse fibres, by the alternate contraction and relaxation of which the food is carried through the canal from above downward, and the arrangement of which varies in different portions of the alimentary tract. The mucous membrane presents, also, a different structure, and has different properties in different parts. That of the mouth and œsophagus is smooth, with a hard, white, tessellated epithelium, which, however, terminates abruptly at the cardiac orifice of the stomach. The mucous membrane of the gastric cavity is soft and glandular, covered with a transparent, columnar epithelium, and thrown into minute folds or projections on its free surface, which are sometimes reticulated with each other. In the small intestine it presents larger transverse folds known as the "valvulæ conniventes," is covered upon its free surface with thickly set villosities of various forms, and contains throughout an abundance of tubular follicles. Finally, in the large intestine the mucous membrane is smooth and shining, free from villosities, and provided with a glandular apparatus different in structure and function from that of the preceding parts.

The digestive secretions, also, vary in these different regions. In its passage from above downward, the food meets with at least five different secreted fluids, namely, the *saliva*, in the cavity of the mouth; the *gastric juice* in the stomach; and the *intestinal juice*, with the *pancreatic juice* and the *bile*, discharged into the cavity of the small intestine. These fluids are themselves, in some instances, of complex nature, resulting from the mingled secretions of several different associated glands, or of the various parts of a single mucous membrane. To a certain extent, the special action of each digestive fluid upon the food has been investigated; and it is found that certain of the secretions have a distinct and peculiar influence upon special ingredients of the food. As the result of the successive action of the digestive fluids, modified, perhaps, by the effect of their combined operation, the substances composing the alimentary mass are gradually reduced to a fluid condition, in which they are fit for absorption by the vessels of the intestinal mucous membrane.

The action which is exerted upon the food by the digestive fluids is not that of a simple chemical solution. It is a transformation, by which the ingredients of the food are altered in character at the same

time that they undergo the process of liquefaction. The active agent in producing this change is in every instance an albuminoid or nitrogenous matter, which forms the most important ingredient in the digestive fluid; and which, by coming in contact with the food, exerts upon it a peculiar action, transforming its ingredients into new substances. It is these newly-formed materials which are finally absorbed by the vessels and mingled with the general current of the circulation. In the human species the first process to which the food is subjected is that of mastication, while it is at the same time mingled with the saliva in the cavity of the mouth.

Mastication.

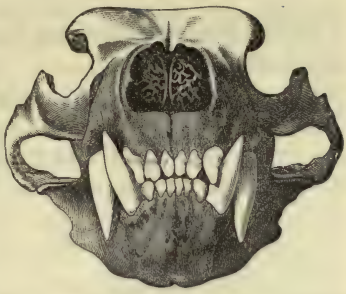
Mastication consists in the cutting and trituration of the food by the teeth, by which it is reduced to a state of minute subdivision. The process is entirely a mechanical one, and is necessary in order to prepare the food for the subsequent action of the digestive fluids. As this action is chemical in its nature, it will be exerted more promptly and efficiently if the food be finely divided than if brought in contact with the digestive fluids in a solid mass. This is necessarily the case when a solid body is subjected to the action of a solvent fluid; since, by being broken up into minute particles, it offers a larger surface to the contact of the fluid, and is more readily attacked and dissolved by it.

In the structure of the teeth, and their physiological action, there are certain marked differences, corresponding with the habits of the animal and the kind of food upon which it subsists. In fish and serpents, in which the food is swallowed entire, and in which the process of digestion, accordingly, is comparatively slow, the teeth are simply organs of prehension. They have generally the form of sharp, curved spines, with their points set backward, and arranged in a double or triple row about the edges of the jaws, and sometimes covering the mucous surfaces of the mouth, tongue, and palate. They serve merely to retain the prey, and prevent its escape, after it has been seized by the animal. In the carnivorous quadrupeds, there are three different kinds of teeth, adapted to different purposes. (Fig. 30.) First, the incisors, twelve in number, situated at the anterior part of the jaw, six in the superior, and six in the inferior maxilla, of flattened form, and placed with their thin edges running from side to side. The incisors, as their name indicates, are adapted for dividing the food by a cutting motion, like that of a pair of shears. Behind them come the canine teeth, or tusks, one on each side of the upper and under jaw. These are long, curved, conical, and pointed; and are used as weapons of offence, and for laying hold of and retaining the prey. Lastly, the

Fig. 29.

SKULL OF RATTLESNAKE.
(Achille Richard.)

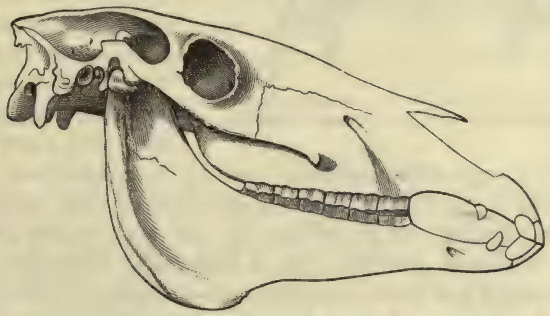
Fig. 30.



SKULL OF POLAR BEAR. Anterior view; showing incisors and canines.

molars, eight or more in number on each side, are larger and broader than the incisors, and provided with serrated edges, each presenting several sharp points, arranged generally in a direction parallel with the line of the jaw. In these animals, mastication is very imperfect, since the food is not ground up, but only pierced and mangled by the action of the teeth before being swallowed into the stomach. In the herbivora, on the other hand, whose food is more easily obtained, but is generally more hard and resisting in texture, the teeth are adapted especially for mastication. In the ruminating animals generally, the canine teeth are wanting, and the incisors are present only in the lower jaw. In the horse and allied species, the incisors are present in both upper and lower jaws (Fig. 31), and are used simply for cutting off the herbage upon which the animal feeds.

Fig. 31.



SKULL OF THE HORSE.

The canine teeth are absent in the female, and only slightly developed in the male, and the real process of mastication is performed altogether by the molars. These are large and thick (Fig. 32), and present a broad, flat surface, diversified by variously folded and projecting ridges of enamel, with shallow grooves between them. By the lateral rubbing motion of the roughened surfaces against each other, the food is effectually comminuted and reduced to a pulpy mass.

Fig. 32.

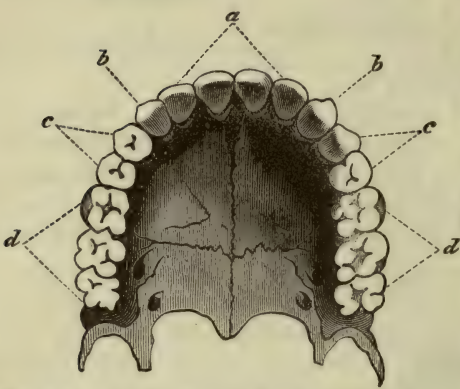
MOLAR TOOTH OF THE HORSE. Grinding surface.

In the gnawing animals, rats, mice, squirrels, rabbits, and hares, the incisor teeth are developed to a remarkable extent, presenting two chisel-like edges opposed to each other in the upper and lower jaws, and growing from permanently vascular roots; so that their waste from mechanical attrition is con-

stantly repaired, and the animal is able to penetrate the hardest substances.

In the human subject, the teeth combine the characters of those of the carnivora and the herbivora. (Fig. 33.) The incisors (*a*), four in number in each jaw, have, as in other instances, a cutting edge running from side to side. The canines (*b*), which are situated immediately behind the former, are much less prominent and pointed than in the carnivora, and differ less in form from the incisors on the one hand, and the first molars on the other. The molars (*c*, *d*) are thick and strong, and have comparatively flat surfaces, like those of the herbivora; but instead of presenting curvilinear ridges, are covered with more or less conical eminences, like those of the carnivora. In the human subject, therefore, the teeth are evidently adapted for a mixed diet, consisting of both animal and vegetable food. Mastication is here as perfect as in the herbivora, though less prolonged and laborious; for the vegetable substances used by man, as already remarked, are previously separated to a great extent from their impurities, and softened by cooking; so that they do not require, for their mastication, so extensive and powerful a triturating apparatus. Finally, animal substances are more completely masticated in the human subject than in the carnivora, and their digestion is accordingly completed with greater rapidity.

Fig. 33.



HUMAN TEETH—UPPER JAW.—*a.* Incisors. *b.* Canines. *c.* Anterior molars. *d.* Posterior molars.

We can easily estimate, from the facts above stated, the importance, to the digestive process, of a thorough preliminary mastication. If the food be hastily swallowed in undivided masses, it must remain a long time undissolved in the stomach, where it will become a source of irritation and disturbance; but if reduced beforehand, by mastication, to a state of minute subdivision, it is readily attacked by the digestive fluids, and becomes speedily and completely liquefied.

The Saliva and its Action upon the Food.

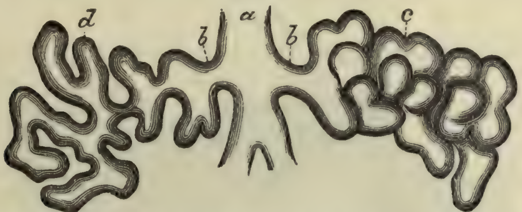
The saliva is a compound fluid, derived from the secretion of four different glandular organs—namely, the parotid, submaxillary, and sublingual glands, and the muciparous glandules of the cavity of the mouth. All these glands resemble each other in the essential points of their

structure, their substance being composed of distinct irregularly spherical or ovoidal masses, more or less flattened into a polygonal form by mutual compression. The separate divisions or *lobules* are connected with corresponding terminal branches of the salivary duct, which penetrate into their interior, and there divide into smaller tubes each one of which finally terminates in a rounded sac called the *glandular follicle* or alveolus. The appearance presented upon an injection of such a lobule is as if the follicles were arranged in clusters, like grapes, around the ends of the smaller salivary tubes. (Fig. 34.) A more complete examination has shown, however, that the follicles are simply the rounded extremities of tubular or sac-like offshoots from the salivary tube; and that it is the windings and prolongations of the tube itself which constitutes the secreting follicles of the gland. The follicles themselves are in general about 50 mmm. in diameter, and are lined with the *glandular epithelium cells*, which cover their internal surface and nearly fill their cavity; so that there is frequently to be seen only a comparatively small space toward the central part of the follicle, containing a transparent fluid, produced by the secreting

Fig. 34.

LOBULE OF PAROTID GLAND of newly-born infant, injected with mercury. (Wagner.)

Fig. 35.



TWO SALIVARY TUBES FROM THE LOBULE OF A MUCIPAROUS GLAND, entering the main duct.—*a.* Duct of the lobule. *b.* Salivary tube. *c.* Follicles, on one side, as they appear *in situ.* *d.* Follicles separated from each other, showing the windings and offshoots of the salivary tube. (Kölliker.)

action of the cells. The glandular cells, which are arranged in a single layer, are finely granular bodies, about 15 mmm. in diameter, each one provided with an oval nucleus, situated toward the external part of the follicle. The cells are closely packed together, and are of various polygonal forms.

The *salivary tubes* or *ducts*, outside the follicles, unite into larger and larger branches, until they reach the principal excretory duct of the gland. They are lined with a layer of cells which vary in form from those of the follicles, being elongated and cylindrical, and provided with a nucleus which is situated about their middle portion. It is very probable that the epithelium of the salivary ducts, as well as that of the follicles, takes

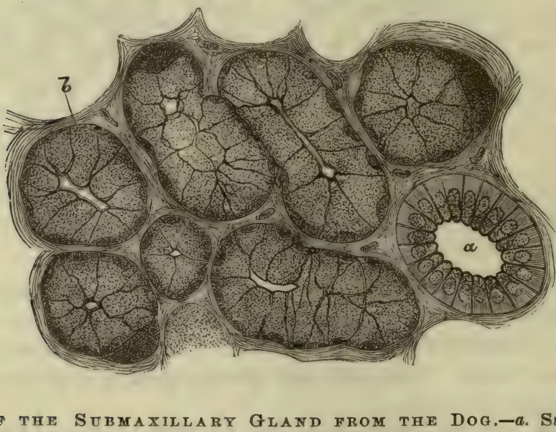
part in the process of secretion; since Pflüger has found that in sections of the gland, examined immediately after being taken out of the

Fig. 36.

Glandular Follicles and Cells; from the submaxillary gland of the dog. (Heidenhain.)

body, transparent drops of fluid may be seen exuding from the ends of the cylindrical epithelium cells into the cavity of the duct. The follicles

Fig. 37.

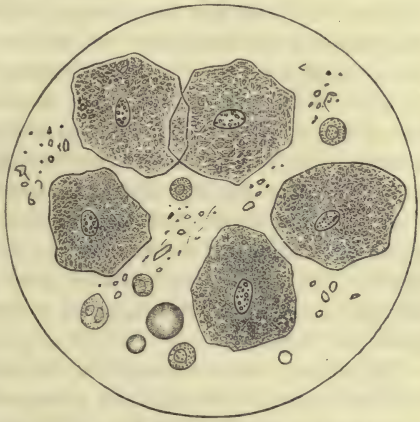


Section of the Submaxillary Gland from the Dog.—*a*. Salivary duct, with cylindrical epithelium and central cavity. *b*. Follicle, with glandular epithelium and central cavity. (Kölliker.)

and lobules are surrounded with a delicate layer of connective tissue, in which are distributed the capillary bloodvessels, which supply to the gland the materials for its secretion.

Physical and Chemical Properties of the Saliva.—Human saliva, obtained directly from the cavity of the mouth, is a colorless, slightly viscid, and alkaline fluid, with a specific gravity of 1.005. When first discharged, it is frothy and opaline, holding in suspension minute whitish flocculi. On being allowed to stand for some hours in a cylindrical glass vessel, an opaque, whitish deposit collects at the bottom, while the supernatant fluid becomes clear. The deposit, when examined by the microscope (Fig. 38), is seen to consist of abundant epithelium scales from the internal surface of the mouth, detached by mechanical attrition, minute, roundish, granular, nucleated cells, apparently epithelium from the mucous follicles, a certain amount of granular matter, and a few oil-globules. The supernatant fluid has a faint bluish tinge, and becomes slightly opalescent by boiling, or by the addition of nitric acid. Alcohol in excess causes the precipitation of abundant whitish flocculi.

Fig. 38.



BUCCAL AND GLANDULAR EPITHELIUM, with Granular Matter and Oil-globules; deposited as sediment from human saliva.

According to the analyses of Bidder and Schmidt, the composition of the saliva is as follows:

COMPOSITION OF THE SALIVA.

Water	995.16
Albuminous matter	1.34
Potassium sulphocyanide	0.06
Calcareous, magnesian, and alkaline phosphates	0.98
Sodium and potassium chlorides	0.84
Mixture of epithelium	1.62
	1000.00

It will be seen that the saliva is one of the least concentrated of the digestive secretions, containing but a very small quantity of organic matter, and by no means a large proportion of mineral salts; its watery ingredient being by far the most abundant, as compared with the other animal fluids. The albuminous matter of the saliva consists of a small quantity of *albumen*, coagulable by the ordinary means; more or less *mucosine*, which gives to the fluid its slightly viscid character; and *ptyaline*, a substance peculiar to the saliva, which is not coagulated, like albumen, by nitric acid or potassium ferrocyanide, but is precipi-

tated both by a boiling temperature and by alcohol in excess. Some of these reagents, accordingly, precipitate all the albuminous matters of the saliva, while others produce coagulation of only a part of them. The sodium sulphocyanide of the saliva may be detected by adding to the secretion a small quantity of a solution of iron chloride, when the characteristic red color of iron sulphocyanide is produced. A similar red color is also produced by the action of the ferric salts upon *meconic acid*, or the meconates; but the two substances may be distinguished from each other by the fact that the red color caused by the presence of a sulphocyanide is destroyed by the addition of either gold chloride or mercurial bichloride, neither of which affects the tint produced by meconic acid. The presence of a combination of sulphocyanogen in human saliva is almost constant, and we have never failed to find it in the freshly collected secretion by the iron-chloride test. Vierordt[1] has calculated the amount of potassium sulphocyanide in saliva by measuring the absorption of light in the green and blue portions of the spectrum of the red fluid produced on the addition of iron chloride; and has found it, in an average of six observations, to be 0.16 parts per thousand.

The saliva, like various other animal fluids, has the property of converting hydrated starch into glucose if mingled with it at or about a temperature of 38° (100° F.). The change is not confined to precisely this temperature, but will go on, with diminished rapidity, both above and below it, if the degree of cold or warmth be not too great. It is entirely suspended, however, at or near the freezing point, and is permanently arrested by the temperature of boiling water. It depends, in the saliva, upon the presence of *ptyaline*, which acts in this respect like the "diastase" of certain vegetable substances. Like other similar matters which exert a so-called "catalytic" action, it will produce its effect only within certain limits of temperature, and is most efficient at about the warmth of the living body. It is affected differently, however, by the action of cold and that of heat; for while a freezing temperature only suspends it for the time being, and allows it to recommence when moderate warmth is again applied, a boiling temperature at once coagulates the ptyaline and destroys its catalytic property. Saliva, therefore, which has been boiled for a few instants and allowed to cool, is found to have permanently lost its power of transforming starch into sugar.

This action of human saliva on hydrated starch takes place sometimes with great rapidity. Traces of glucose may often be detected in the mixture in one minute after the two substances have been brought in contact; and we have even found that starch paste, introduced into the cavity of the mouth, if already at the temperature of 38°, will yield traces of sugar at the end of half a minute. The rapidity, however, with

[1] Anwendung des Spectralapparates zur Photometrie der Absorptionsspectren. Tübingen, 1873, p. 147.

which this action is manifested, varies very much, as formerly noticed by Lehmann, at different times; and it is frequently impossible, even with the mixture kept steadily at the temperature of 38°, to find any evidence of sugar under five, ten, or fifteen minutes. This difference depends probably upon the varying constitution of the saliva itself.

Notwithstanding the rapidity with which glucose begins to show itself in a mixture of saliva with boiled starch, this action is not a very energetic one; that is, only a very small quantity of the starch is converted into glucose within a given time, the greater portion remaining unchanged. This is proved by the fact that such a mixture will show the characteristic reaction of starch with iodine long after Fehling's test has shown the existence of traces of glucose. If a weak solution of boiled starch, made in the proportion of 3 parts of starch to 100 parts of water, be mixed with one-third of its volume of fresh human saliva and placed in the water-bath at the temperature of 38°, it will often give, in one minute, a prompt sugar-reaction with Fehling's test; but it also contains, at the same time, an abundance of unaltered starch. Even at the end of an hour, according to our own observations, the starch is far from being entirely converted, as the mixture will still give a strong purple-blue color on the addition of iodine. The same persistence of starch in considerable proportion may be seen when the mixture is retained in the mouth itself. If a thin paste of hydrated starch, containing no traces of sugar, be taken into the mouth and thoroughly mixed with the buccal secretions, it will often, as above mentioned, begin to show the reaction of glucose in half a minute; but some of the starchy matter still remains, and will continue to manifest its characteristic reaction with iodine for fifteen or twenty minutes, or even for half an hour.

The secretions produced by the different salivary glands vary somewhat in their physical properties, especially in the degree of their viscidity, depending mainly upon the quantity of mucosine present. The *parotid* saliva is obtained in a state of purity from the dog by exposing the duct of Steno where it crosses the masseter muscle, and introducing into it, through an artificial opening, a silver canula. The secretion then runs directly from its external orifice, without being mixed with that of the other salivary glands. It is clear, limpid, and watery, and without the slightest viscidity. The *submaxillary* saliva is obtained in a similar manner, by inserting a canula into Wharton's duct. It differs from the parotid secretion, so far as its physical properties are concerned, chiefly in possessing a well marked viscidity. The *sublingual* saliva is also colorless and transparent, and possesses a greater degree of viscidity than that from the submaxillary. The secretion of the muciparous glandules, which forms properly a part of the saliva, is obtained by placing a ligature simultaneously on Wharton's and Steno's ducts, and on that of the sublingual gland, so as to shut out from the mouth all the glandular salivary secretions, and then collecting the fluid secreted by the buccal mucous membrane. This fluid is very scanty, and

much more viscid than either of the other secretions; so much so, that it cannot be poured out in drops when received in a glass vessel, but adheres strongly to the surface of the glass. All the salivary secretions are alkaline in reaction.

We have obtained the *parotid saliva of the human subject* in a state of purity by introducing directly into the orifice of Steno's duct a silver canula a little over one millimetre in diameter. The other extremity of the canula projects from the mouth between the lips, and the saliva is collected as it runs from the open orifice. This method gives results much more valuable than observations made on salivary fistulæ and the like, since the secretion is obtained under perfectly healthy conditions, and unmixed with other animal fluids.

The result of many different observations, conducted in the manner above described, is that the human parotid saliva, like that of the dog, is colorless, watery, and distinctly alkaline in reaction. It differs from the mixed saliva of the mouth, in being perfectly clear, without turbidity or opalescence. Its flow is scanty while the cheeks and jaws remain at rest; but as soon as the movements of mastication are excited by the introduction of food, it runs in much greater abundance. We have collected, in this way, from the parotid duct of one side only, in a healthy man, 31.1 grammes of saliva in the course of twenty minutes; and in seven successive observations, made on different days, comprising in all three hours and nine minutes, we have collected a little over 194 grammes.

The parotid saliva obtained in this way has been analyzed by Prof. Maurice Perkins, with the following result:

COMPOSITION OF HUMAN PAROTID SALIVA.

Water	983.308
Organic matter precipitable by alcohol	7.352
Substance destructible by heat, but not precipitated by alcohol	4.810
Sodium sulphocyanide	0.330
Lime phosphate	0.240
Potassium chloride	0.900
Sodium chloride and carbonate	3.060
	1000.000

Prof. Perkins found, in accordance with our own observations, that the fresh parotid saliva, when treated with iron chloride, showed no evidences of sulphocyanogen; but after the organic matters had been precipitated by alcohol, the filtered fluid was found to contain an appreciable quantity of sulphocyanide.

The parotid saliva, accordingly, differs from the mixed saliva of the mouth in containing some substance which masks the reaction of sulphocyanogen. If the parotid saliva and that from the mouth be drawn from the same person within the same hour, the addition of iron chloride will produce a distinct red color in the latter, while no such change takes place in the former. And yet the parotid saliva itself contains a

sulphocyanide which may be detected, as we have seen, after the organic matters have been precipitated by alcohol.

Both the parotid saliva and that from the submaxillary gland in the human subject contain ptyaline, but they differ considerably, as in the case of the lower animals, in their degree of viscidity.

Mode of Secretion of the Saliva.—The different salivary glands vary in the quantity of fluid secreted by them and in the different influences which excite them to activity. As shown by Bernard, the parotid saliva is most abundantly poured out under the stimulus of anything which excites the movement of the jaws, as in the mastication of dry substances, or continuous speaking; while that of the submaxillary is especially increased by the introduction of substances which excite the sense of taste. According to the same experiments, the secretion of the sublingual glands in the dog is particularly excited at the moment of deglutition, and aids, together with that of the muciparous glandules, in lubricating the surface of the mouth and fauces, and in facilitating the passage of the masticated food through the œsophagus. Colin, in experimenting upon the horse and the ox,[1] found also that the parotid saliva in these animals is abundantly excited by the movements of mastication, but not by the simple contact of sapid substances with the mucous membrane of the mouth; while, on the other hand, the secretion of the submaxillary saliva is considerably increased by introduction into the mouth of substances having a marked taste. Both the parotid and submaxillary secretions are abundant while the animal is feeding, their quantity being proportional to the rapidity of mastication and the sapid quality of the alimentary substances. They are both either suspended or very much diminished during abstinence. In the ruminants, however, the sublingual saliva, like the submaxillary, is excited by sapid substances; it is also secreted continuously while the animal is feeding, and not simply at the moment of deglutition. It continues to be secreted during abstinence, and contributes to the supply of fluid by which the surfaces are kept in a moist condition.

Another fact observed by Colin which indicates the different nervous influences by which the salivary glands are controlled, is that in the ruminant animals while feeding both the parotid and submaxillary glands furnish an abundant supply of saliva; but during the process of rumination, although the parotid glands are in full secretion, discharging frequently as much as 900 grammes of saliva in a quarter of an hour, the submaxillary glands are entirely inactive or produce only an insignificant quantity of fluid. Colin has also found that in the horse and ass, as well as in the ox and other ruminating animals, the parotid glands of the two opposite sides, during mastication, are never in active secretion at the same time; but that they alternate with each other, one remaining quiescent while the other is active, and *vice versâ*. In these animals mastication is said to be *unilateral*, that is, when the animal commences

[1] Physiologie comparée des Animaux Domestiques. Paris, 1854, tome i. p. 468.

feeding or ruminating, the food is triturated for fifteen minutes or more by the molars of one side only. It is then changed to the opposite side; and for the next fifteen minutes mastication is performed by the molars of that side only. It is then changed back again, and so on alternately, so that the direction of the lateral movements of the jaw may be reversed many times during the course of a meal. By establishing a salivary fistula simultaneously on each side, it is found that the flow of saliva corresponds with the direction of the masticatory movement. When the animal masticates on the right side, it is the right parotid which secretes actively, while but little saliva is supplied by the left; when mastication is on the left side, the left parotid pours out an abundance of fluid, while the right is nearly inactive.

We have observed a similar alternation in the flow of parotid saliva in the human subject, when mastication is changed from side to side. In an experiment of this kind, the tube being inserted into the parotid duct of the left side, the quantity of saliva discharged during twenty minutes, while mastication was performed mainly on the opposite side of the mouth, was 8.26 grammes; while the quantity during the same period, mastication being on the same side of the mouth, was 24.25 grammes—being nearly three times as much in the latter case as in the former.

Daily Quantity of the Saliva.—Owing to the physiological variations in the rapidity of secretion of the saliva, and also to the fact that it is not excited in the same way by artificial stimulus as by the presence of food, it is somewhat difficult to ascertain with exactness its total daily quantity. The first attempts to do so were made upon patients affected with fistula of the parotid duct, and the amounts collected were so small as to lead to the conclusion that the entire quantity secreted by all the glands was not more than ten or twelve ounces, or about 350 grammes per day. As in these cases, however, the subjects of experiment were not in a healthy condition, and as the proportion in quantity between the parotid saliva and that secreted by the remaining glands must necessarily be a matter of conjecture, the above calculation could hardly be regarded as correct. Bidder and Schmidt,[1] from the results of direct observation, were led to make a higher estimate. One of these observers, in experimenting upon himself, collected from the mouth in one hour, without using any artificial stimulus, 97 grammes of saliva; and calculates, therefore, the amount secreted daily, making an allowance of seven hours for sleep, as not far from 1620 grammes.

On repeating this experiment we have not been able to collect from the mouth, without artificial stimulus, more than 36 grammes of saliva per hour. This quantity, however, may be greatly increased by the introduction into the mouth of any smooth unirritating substance, as glass beads or the like; and during the mastication of food, the saliva is poured out in very much greater abundance. The sight and

[1] Verdauungssaefte und Stoffwechsel. Leipzig, 1852, p. 1

odor of nutritious food, when the appetite is excited, will stimulate to a remarkable degree the flow of saliva; and, as it is often expressed, "bring the water into the mouth." Any estimate, therefore, of the total quantity of saliva, based on the amount secreted in the intervals of mastication, would be imperfect. We may make a tolerably accurate calculation, by ascertaining how much is really secreted during a meal, over and above that which is produced at other times. We have found, by experiments performed for this purpose, that wheaten bread gains during complete mastication 55 per cent. of its weight of saliva; and that fresh cooked meat gains, under the same circumstances, 48 per cent. of its weight. We have already seen that the daily allowance of these two substances, for a man in full health and activity, is about 540 grammes of bread and 450 grammes of meat. The quantity of saliva, accordingly, employed in the mastication of these two substances is, for the bread 297 grammes, and for the meat 216 grammes. If we now calculate the quantity secreted between meals as continuing for twenty-two hours at the rate of 36 grammes per hour, we have:

Saliva required for the mastication of bread	= 297	grammes.
" " " " " " meat	= 216	"
" secreted in intervals of meals	= 792	"
Total quantity per day, a little over	1300	"

Physiological Action of the Saliva.—The principal function of the saliva is undoubtedly to moisten the food and provide in this way for its further solution, and especially to assist in mastication, by which the food is converted into a pultaceous mass. This is mainly accomplished by the watery ingredients of the secretion, while the albuminous matters contained in it not only aid in giving to the masticated food the requisite consistency, but also act by lubricating its surface, and facilitating its deglutition. This is evident from the fact that the principal trouble which results from absence or deficiency of the saliva is a difficulty in the mechanical processes of mastication and swallowing. Food which is hard and dry, like crusts or crackers, cannot be masticated and swallowed with readiness, unless moistened by some fluid. If the saliva be prevented from entering the cavity of the mouth, its loss does not interfere directly with the chemical changes of the food in digestion, but only with its physical preparation. This is the result of direct experiments performed by various observers. Bidder and Schmidt,[1] after tying Steno's duct, together with the common duct of the submaxillary and sublingual glands on both sides in the dog, found that the immediate effect of such an operation was "a remarkable diminution of the fluids which exude upon the surfaces of the mouth; so that these surfaces retained their natural moisture only so long as the mouth was closed, and readily became dry on exposure to the air. Accordingly, deglutition became evidently difficult and labo-

[1] Verdauungssaefte und Stoffwechsel, p. 3.

rious, not only for dry food, like bread, but even for that of a tolerably moist consistency, like fresh meat. The animals also became very thirsty, and were constantly ready to drink."

Bernard[1] also found that the only marked effect of cutting off the flow of saliva from the mouth was a difficulty in the mechanical processes of mastication and deglutition. He first administered to a horse 500 grammes of oats, in order to ascertain the rapidity with which mastication would naturally be accomplished. The above quantity of grain was thoroughly masticated and swallowed at the end of nine minutes. An opening had been previously made in the œsophagus at the lower part of the neck, so that none of the food reached the stomach; but each mouthful, as it passed down the œsophagus, was received at the œsophageal opening and examined by the experimenter. The parotid duct on each side of the face was then divided, and another similar quantity of oats given to the animal. Mastication and deglutition were both found to be immediately retarded. The alimentary masses passed down the œsophagus at longer intervals, and their interior was no longer moist and pasty, as before, but dry and brittle. Finally, at the end of twenty-five minutes, the animal had succeeded in masticating and swallowing only about three-quarters of the quantity which he had previously disposed of in nine minutes.

It appears from the experiments of Magendie, Bernard, and Lassaigne, on horses and cows, that the quantity of saliva absorbed by the food during mastication is in direct proportion to its hardness and dryness, but has no particular relation to its chemical qualities. These experiments were performed as follows: The œsophagus was opened at the lower part of the neck, and a ligature placed upon it, between the wound and the stomach. The animal was then supplied with a previously weighed quantity of food, and this, as it passed out by the œsophageal opening, was received into appropriate vessels and again weighed. The difference in weight, before and after swallowing, indicated the quantity of saliva absorbed by the food. The following table gives the results of some of Lassaigne's experiments, performed upon a horse.

Kind of Food employed.		Quantity of Saliva absorbed.
For 100 parts of	hay	400 parts.
"	barley meal	186 "
"	oats	113 "
"	green stalks and leaves	49 "

It is evident from the above facts, that the quantity of saliva produced has not so much to do with the chemical character of the food as with its physical condition. When the food is dry and hard, and requires much mastication, the saliva is secreted in abundance; when it is soft and moist, a smaller quantity of the secretion is poured out; and finally, when the food is taken in a fluid form, as soup or milk, or reduced to powder and moistened artificially with a large quantity of

[1] Leçons de Physiologie Expérimentale. Paris, 1856, p. 146.

water, it is not mixed at all with saliva, but passes at once into the cavity of the stomach.

A difference of opinion exists among various authors as to whether the transforming power of the saliva upon starch be also an essential part of its physiological action. If the digestion of the food took place in the cavity of the mouth, or if it were retained there for any considerable time, there would be no doubt in this respect. But in reality the food is in only momentary passage though the mouth, remaining there merely long enough to allow for mastication. We have already seen that this time is too short to complete the conversion into glucose of even the small quantity of starch contained in a dilute solution, much more so the abundant semi-solid starchy matters of bread or vegetables. There can be no question whatever that in point of fact, the starchy elements of the food are not digested or transformed to any considerable extent while in the cavity of the mouth. They are swallowed into the stomach with by far their greater portion still unchanged. Some observers (Schiff, F. G. Smith, Flint, Ranke, Brunton) believe that the transforming action of the saliva, which is commenced in the mouth, may continue subsequently in the stomach in presence of the gastric juice. Others (Bernard, Robin, Colin) assert that the action of the saliva on starch is arrested by the gastric juice, and, as a matter of fact, does not go on in the stomach. This discrepancy no doubt depends partly upon differences in the mode of experimentation; some writers contenting themselves with testing the effect of dilute acids only on the saliva, others using the gastric juice itself. The proportion in which the two secretions are mingled also makes a difference in the result, and the properties of either one may vary somewhat according to the time at which it is collected. Our own observations lead to the conclusion that gastric juice certainly interferes with the chemical action of saliva, usually to a very marked degree, when mingled with it in equal volumes. If we take fresh unfiltered human saliva, which is shown by a preliminary experiment to be capable of producing a prompt sugar-reaction in a solution of boiled starch at the end of one minute, mix it with an equal volume of freshly collected gastric juice from the dog, then add the starch-solution, and place the mixture in the water-bath at the temperature of 38° (100° F.), there is no sugar-reaction whatever at the end of five minutes, and only an imperfect one in half an hour; while at the end of an hour there may be distinct reduction by Fehling's test.[1] But if three volumes of gastric juice be added for one volume of saliva, the mixture gives no indication of sugar even at the end of an hour. As all observations tend to show that the gastric juice is naturally secreted in much larger quantity than the saliva, these proportions undoubtedly indicate, more nearly than

[1] In these examinations the fluid mixture is always treated with animal charcoal previously to applying Fehling's test; otherwise the albuminous matter of the secretions would interfere with its certainty.

the former, the relative quantities in which the two secretions are present in the stomach during ordinary digestion.

Experiments upon the lower animals, provided with gastric fistulæ, show furthermore that in them starch is not, in point of fact, converted into sugar in the stomach. In the dog, the horse, the sheep, and the ox, according to Bernard, Schiff, and Colin, the action of saliva upon hydrated starch is distinct, though less rapid than that of the human subject. In the gnawing animals generally it is present, and in the guinea pig, according to Schiff, is more decided than in man. But if a dog, with a gastric fistula, be fed with a mixture of meat and boiled starch, and portions of the fluid contents of the stomach withdrawn afterward through the fistula, the starch is easily recognizable by its reaction with iodine for ten, fifteen, and twenty minutes afterward. In forty-five minutes it is diminished in quantity, and in one hour has usually disappeared; but no sugar is to be detected at any time. Sometimes the starch disappears more rapidly than this; but at no time, according to our observations, is there any indication of the presence of sugar in the gastric fluids. Bernard[1] has shown the same want of transformation in the dog's stomach after swallowing a mixture of hydrated starch with ordinary food. Brücke,[2] in dogs fed with starch paste, found in the stomach more or less unchanged starch, and either no sugar or only traces of it, after the lapse of from one to five hours. This does not depend upon any want of power in dogs to digest hydrated starch, since this substance is converted into glucose in these animals with great promptitude on arriving in the duodenum, by the influence of the pancreatic and intestinal juices.

It is also an important consideration, in this respect, that the saliva exerts its transforming power only upon starch which has been cooked or hydrated. All observers agree that it is nearly or quite without action upon raw starch, which remains unchanged in contact with it at all temperatures. But in the herbivorous animals, where the salivary glands are at least as fully developed and the saliva as abundant as in man, the starchy elements of the food are habitually taken in the raw state. Even in the ruminating animals, where the food is retained, for some time after the first mastication, in the paunch, unmixed with gastric juice, it does not undergo there the sugar-conversion. Prof. Francis G. Smith, in a series of experiments upon Alexis St. Martin, affected with a gastric fistula, in 1856,[3] withdrew the contents of the stomach two and a half hours after bread had been masticated and swallowed; and in the mixed fluids so obtained, he detected at the end of that time unchanged starch, both by the microscope and by the iodine test. Glucose was also found in the fluid, but, as bread nearly always contains glucose, it is uncertain how much,

[1] Sécrétions Digestives. Paris, 1856, p. 159.

[2] Jahresberichte der Anatomie und Physiologie. Leipzig, 1873, p. 467.

[3] Philadelphia Medical Examiner, July and September, 1856.

if any, had been produced by transformation of the starch. Colin[1] has found the farinaceous matter of oats and of starchy roots recognizable by its iodine reaction, after these substances had remained in the first stomach of the ox, mixed with saliva, for twenty-four hours. The same observer introduced into the interior of the paunch, through a fistula, small muslin bags containing uncooked potato starch, which were found in the same cavity, still full of unaltered starch, at the end of twenty and twenty-two hours. It is worth remembering furthermore that the salivary glands and their secretion are also abundantly developed in the carnivora, whose food never in the natural condition contains starch as an ingredient.

It appears evident, therefore, that the chemical action of the saliva in the lower animals forms no part of the natural process of digestion; and that in man it is insignificant in amount, and quite subordinate to that of other digestive fluids. In both animals and man, however, and in the carnivora as well as in the herbivora, its physical properties are important in accomplishing the processes of mastication and deglutition.

Mastication is aided and controlled in great measure by the sensibilities of touch and taste, residing in the surface of the tongue and other parts of the mucous membrane. The sense of taste notifies us of the alimentary qualities of the food taken into the mouth, and its sapid qualities must be fully brought out by the comminution and moistening of the food before mastication is complete. The taste itself depends, for one of its essential conditions, upon a sufficient supply of saliva, and this is by no means an unimportant function of the secretion. No substance can produce an impression upon the nerves of taste unless it be in a fluid form and capable of absorption by the mucous membrane. The saliva produces this effect upon the soluble ingredients of the food, and brings them in contact with the papillæ of the tongue in sufficient quantity to produce a gustatory sensation.

The general sensibility of the tongue, which is highly developed, also enables this organ to appreciate the physical condition of the food and how far it is prepared for deglutition. At the same time its muscular apparatus provides for its movement in every direction. When the alimentary material is finally reduced, by mastication and mixture with the saliva, to a sufficiently pasty and homogeneous condition, the softened mass is collected from every part of the mouth by the movements of the tongue and brought together upon its upper surface. It is then pressed backward by the muscular force of the organ, and carried through the fauces into the pharynx and upper part of the œsophagus. Here it passes beyond the control of the will. It is then grasped by the muscular fibres of the œsophagus, and by the continuous and rapid peristaltic action of this canal is carried downward into the stomach.

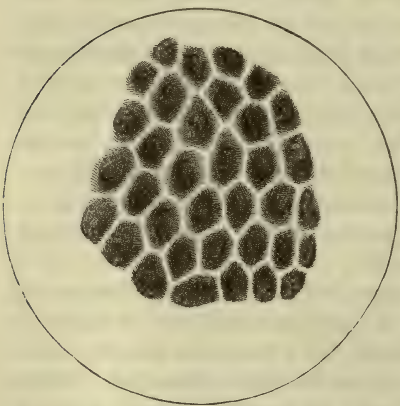
[1] Physiologie comparée des Animaux Domestiques. Paris, 1854, tome i. p. 603.

The Gastric Juice and Stomach Digestion.

The stomach has long been recognized as the organ in which the most important part of the digestive process is inaugurated, and in which the essential chemical modifications of the alimentary matters first take place. Its action consists in the production of a special digestive fluid, the *gastric juice*, furnished by the glandular apparatus of its mucous membrane.

The gastric mucous membrane presents certain variations, both in its general appearance and its intimate structure, in different portions of the stomach. It is red in the cardiac and middle portion, paler in the cardiac portion. It increases also in thickness from the cardia toward the pylorus; being, according to the measurements of Kölliker, about half a millimetre thick in the cardiac portion, one millimetre in the middle, and one and a half to two millimetres near the pylorus. Its free surface is everywhere more or less uneven and marked with minute ridges or eminences. In the cardiac portion (Fig. 39) these ridges are reticulated with each other, so as to include between them polygonal interspaces, each of which is encircled by a network of capillary bloodvessels. In the pyloric portion Fig. 40) the eminences are more distinct

Fig. 39.



Free surface of GASTRIC MUCOUS MEMBRANE, viewed from above; from Pig's Stomach, Cardiac portion. Moderately magnified.

Fig. 40.

Free surface of GASTRIC MUCOUS MEMBRANE, viewed in vertical section; from Pig's Stomach, Pyloric portion. More highly magnified.

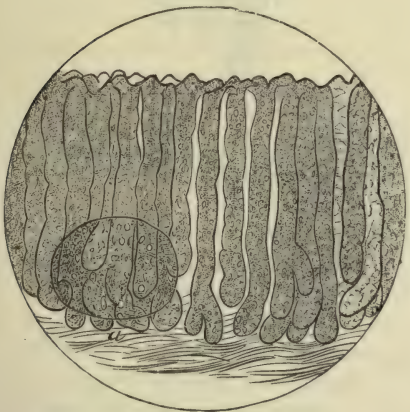
from each other, pointed in form, about one-tenth of a millimetre in height, and generally flattened from side to side. In the human subject these villus-like projections have even been found extending over the whole surface of the gastric mucous membrane. Each one contains a capillary bloodvessel, which returns upon itself in a loop at the extremity of the projection, and communicates freely with adjacent vessels.

The entire thickness of the mucous membrane of the stomach consists of *glandular follicles* or tubules, some of which are simple in structure,

while others are compound or branched. Another distinction between the follicles is that some of them are lined throughout with cylindrical epithelium cells, not very different from those on the free surface of the mucous membrane, while others contain also larger cells of a rounded form, which give to the follicles a peculiar aspect. Both simple and branched follicles may be found, presenting both these two kinds of epithelium; but as a general rule, the simple tubular follicles are distinguished by their lining of cylindrical epithelium, while the compound or branched follicles more especially contain the larger cells of glandular epithelium.

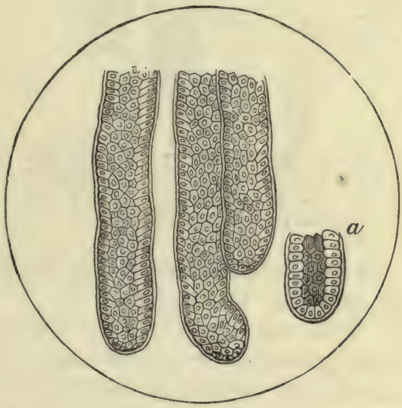
In the pyloric portion of the stomach, the follicles with cylindrical epithelium preponderate, or in some instances are present exclusively. In the dog, according to the observations of Ebstein, and in man, according to Kölliker, the mucous membrane in the immediate proximity of the pylorus, for a zone of considerable width, contains follicles of this kind only. They present the same essential characters in man and in different species of animals. They are nearly straight or slightly tortuous tubules, $\frac{1}{16}$ of a millimetre in diameter, lined with cylindrical epithelium cells, and terminating in blind extremities at the under surface of the mucous membrane (Fig. 41). In their lower half they are

Fig. 41.



MUCOUS MEMBRANE OF PIG'S STOMACH, from Pyloric portion; vertical section; showing tubular follicles, and, at *a*, a closed follicle. Moderately magnified.

Fig. 42.



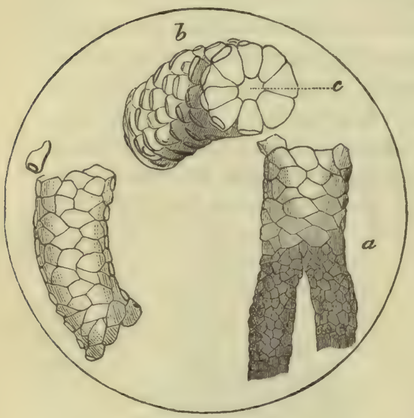
TUBULAR FOLLICLES, from Pyloric portion of Pig's Stomach, showing their cœcal extremities and epithelial lining. At *a*, the torn end of a follicle, showing its cavity. More highly magnified.

often slightly branched, one or more lateral diverticula passing off from the principal tubule, and forming a little mass or lobule of glandular tubes. At their upper extremities they open on the free surface of the mucous membrane, in the interspaces between the projecting folds or villi. The cylindrical epithelium cells, which cover the general surface of the gastric mucous membrane, extend downward into the cavity of

the follicles and reach even to their blind extremities (Fig. 42); only in the interior of the follicles they are shorter, less transparent, and more glandular in appearance than on the free surface of the mucous membrane.

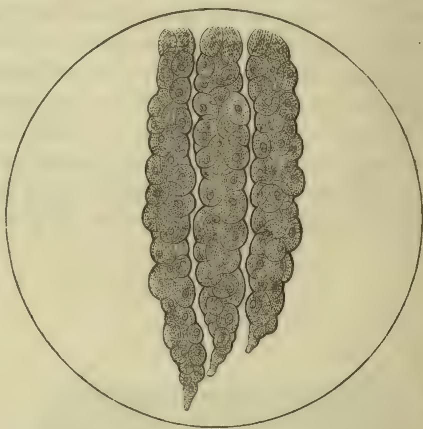
In the cardiac portion of the stomach the superficial part of the mucous membrane contains wide depressions or tubes, lined with large cylindrical epithelium cells. These tubes, at a short distance below the surface, are joined each by two or more tubular follicles, lined with small glandular epithelium cells, and terminating below, like the preceding, in rounded extremities (Fig. 43).

Fig. 43.



GASTRIC FOLLICLES, from Pig's Stomach, Cardiac portion. At *a*, two follicles joining a larger tube; *b*, portion of a tube seen endwise; *c*, its central cavity.

Fig. 44.



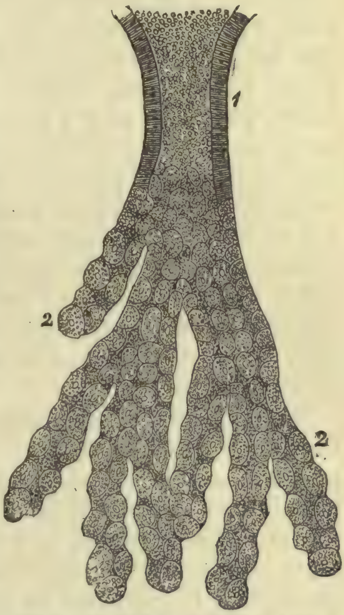
GASTRIC FOLLICLES, with large glandular cells; from middle portion of Pig's Stomach.

In the mucous membrane of both the fundus and middle portion of the stomach, but especially in the middle portion, there are follicles which are distinguished by containing, in addition to the cylindrical or small glandular epithelium cells, larger spheroidal cells of peculiar aspect. As already mentioned, these follicles are usually compound, but they are also met with of a simple tubular form. The spherical cells which they contain are usually most abundant in their lower portions, but are often more distinctly defined in the middle part of the follicle. These cells are rounded in form, about 20 mmm. in diameter, finely granular, and provided with well-marked oval nuclei. They nearly fill the cavity of the follicle, and also project laterally from its external surface, giving to it from this cause an extremely characteristic varicose or irregularly tumefied appearance (Fig. 44). In the compound follicles of the cardiac portion of the human stomach (Fig. 45), the spherical cells are found more or less abundantly throughout their deeper and middle

parts, up to the point where they join the wider tube leading to the surface.

These spheroidal cells have been designated by the name of "pepsine cells," and the glandular follicles containing them as "peptic glands," from a supposition that they are exclusively concerned in the production of the essential organic ingredient of the gastric juice. Opinions, however, are divided upon this point. The follicles in question contain both the so-called "pepsine cells" and the smaller cells of glandular epithelium; the two kinds of cells being found associated in the same follicles over a large portion of the stomach. It is only in the pyloric region that the follicles contain cells of the smaller variety alone. It is acknowledged by all that by the action of glycerine a substance having the properties of pepsine may be extracted from the middle or cardiac portions of the gastric mucous membrane, and not from the pyloric portion. But Ebstein has shown[1], that, if two digestive fluids be prepared by macerating the gastric mucous membrane in water acidulated with hydrochloric acid, using for one the pyloric portion and for the other the middle portion, both of these fluids possess under similar conditions, digestive properties which are the same in kind, and differ only in degree. The principal distinction between the two kinds of cells, according to the same observer, is that the substance of the cylindrical cells becomes cloudy and shrivelled by the action of acids generally; while that of the spheroidal cells is thus affected only by mineral acids, acetic acid, on the contrary, causing them to become swollen and transparent. From this it is concluded that the smaller cells contain a substance like mucosine, while the larger consist of materials more closely resembling albumen.

Fig. 45.



COMPOUND GASTRIC FOLLICLE, from the Cardiac portion of human stomach. 1. Excretory tube, leading to the surface. 2. Tubular follicles, containing spheroidal cells. (Kölliker.)

It cannot therefore be said with certainty, that either the larger cells or the follicles containing them produce exclusively either the pepsine or the acid of the gastric juice. No doubt the follicles in different portions of the stomach differ from each other more or less, in function as well as in appearance; but it is not yet possible to determine the exact nature of the differences between them. By the combined action of all

[1] Archiv für Mikroskopische Anatomie, 1870, vi. p. 515.

parts of the glandular apparatus is produced the characteristic secretion of the gastric juice.

Physical Qualities and Composition of the Gastric Juice.—The earliest decisive investigations in regard to the existence and properties of the gastric juice were those made by Dr. Beaumont, of the United States Army, in the case of Alexis St. Martin, a Canadian boatman, who was affected with a permanent gastric fistula, the result of an accidental gun-shot wound. The musket, which was loaded with buckshot at the time of the accident, was discharged, at the distance of a few feet from St. Martin's body, in such a manner as to tear away the integument at the lower part of the left chest, open the pleural cavity, and penetrate, through the lateral portion of the diaphragm, into the great pouch of the stomach. After the integument and the pleural and peritoneal surfaces had united and cicatrized, there remained a permanent opening about two centimetres in diameter leading into the left extremity of the stomach, which was usually closed by a circular valve of protruding mucous membrane. This valve could be readily depressed at any time, so as to open the fistula and allow the contents of the stomach to be extracted for examination.

Dr. Beaumont experimented upon this person at various intervals from the year 1825 to 1832.[1] He established during the course of his examinations the following important facts: First, that the active agent in digestion is an acid fluid, secreted by the walls of the stomach; secondly, that this fluid is poured out by the glandular walls of the organ only during digestion, and under the stimulus of the food; and finally, that it will exert its solvent action upon the food outside the body as well as in the stomach, if kept in glass phials upon a sand-bath at the temperature of 38° (100° F.). He made also a variety of other interesting investigations as to the effect of various kinds of stimulus on the secretion of the stomach, the rapidity with which the process of digestion takes place, and the comparative digestibility of various kinds of food.

The same person, with his gastric fistula unchanged, after an interval of twenty-four years, came under the observation of Prof. Francis G. Smith, of the University of Pennsylvania, who again made a series of important experiments of a similar nature, confirming and extending those of Dr. Beaumont; and another case, in a young and otherwise healthy woman, the result of a local inflammation and abscess, happened in Germany in 1854, and was investigated by Prof. C. Schmidt.

Since Dr. Beaumont's time similar experiments have been frequently performed by means of gastric fistulæ artificially established upon the lower animals, especially upon the dog, which has been found most convenient for this purpose; the result of examinations conducted by this and other methods being that the gastric juice presents the same essential characters in man and in the carnivorous and herbivorous

[1] Experiments and Observations upon the Gastric Juice. Boston, 1834.

animals. The simplest and most effectual mode of establishing a gastric fistula in the dog is the following: A longitudinal incision, about six centimetres in length, is made through the abdominal parietes in the median line, over the great curvature of the stomach. The anterior wall of the organ is then to be seized with a pair of hooked forceps, drawn out at the external wound, and opened with the point of a bistoury. A short silver canula from one to two centimetres in diameter, armed at each extremity with a narrow projecting rim or flange, is inserted into the wound in the stomach, the edges of which are fastened round the tube with a ligature in order to prevent the escape of the gastric fluids into the peritoneal cavity. The stomach is then returned to its place in the abdomen, and the canula allowed to remain with its external flange resting upon the edges of the wound in the abdominal integuments, which are to be drawn together by sutures. The animal may be kept perfectly quiet, during the operation, by the administration of ether or chloroform. In a few days the ligatures come away, the wounded peritoneal surfaces unite with each other, and the canula is retained in a permanent gastric fistula; being prevented by its flaring extremities both from falling out of the abdomen and from being accidentally pushed into the stomach. It is closed externally by a cork, which may be withdrawn at pleasure, and the contents of the stomach thus obtained for examination.

Experiments conducted in this manner confirm, in the main, the results obtained by Dr. Beaumont. Their results are even, in some respects, more satisfactory than those obtained from the human subject; since animals are more completely under the control of the experimenter, and all sources of deception or mistake are thereby avoided, while the investigation is, at the same time, facilitated by the simple character of the food administered.

The gastric juice obtained by this method is a clear, colorless, or faintly amber-colored fluid, of a perfectly watery consistency and a distinctly acid reaction. Its specific gravity does not vary much from 1010. It becomes slightly opalescent on boiling.

The following is the composition of the gastric juice of the dog, based upon a comparison of various analyses by Lehmann, Blondlot, Otto, Bidder and Schmidt.

COMPOSITION OF GASTRIC JUICE.

Water	975.00
Free acid	4.78
Pepsine	15.00
Sodium chloride	1.70
Potassium "	1.08
Calcium "	0.20
Ammonium "	0.65
Lime phosphate	1.48
Magnesium "	0.06
Iron "	0.05
	1000 00

Prof. C. Schmidt[1] found the gastric juice of the human subject similar in constitution to the above, except that it contained a larger proportion of water and a considerably smaller proportion both of free acid and pepsine, as well as of solid ingredients generally. From our own repeated observations upon the dog, there is no doubt that both the quantity and density of the gastric juice vary, within certain limits, in different individuals even of the same species—the proportion of solid ingredients being less when the secretion is more abundant, and greater when the secretion is in small quantity.

The most striking physical property of the gastric juice is its acid reaction, which is always strongly marked, and by which it is distinguished from all the other digestive secretions and internal fluids of the body. This property, as indicated in the foregoing table, depends upon the presence in the secretion of a *free acid.* Notwithstanding the numerous investigations which have been directed to this point, it is still uncertain whether the reaction of the gastric juice be due to free hydrochloric or free lactic acid; each of these two substances having been found by different observers. Those who attribute the reaction of the gastric juice to hydrochloric acid (Prout, Dunglison, Enderlin, Bidder and Schmidt) depend upon its being obtainable by distillation, and more especially upon a quantitative determination of all the alkaline and earthy bases contained in the secretion, and an estimate of the amount of hydrochloric acid necessary to saturate these bases; the hydrochloric acid, actually obtainable, being found to be more than sufficient to unite with the above bases in neutral combination. On the other hand, various experimenters (Lehmann, Leuret, Lassaigne, Francis G. Smith, Bernard and Barreswil) have not only found evidences of the presence of free lactic acid in the gastric juice, but some of them have also shown[2] that during distillation the concentrated lactic acid would set free hydrochloric acid by decomposition of the alkaline chlorides, although none were originally present in the fluid. They also point out that the addition of a small quantity of oxalic acid to the gastric juice produces a precipitate of lime oxalate, while no such precipitation will take place in a fluid containing two parts per thousand of free hydrochloric acid. It is certain, however, that either of these acids may replace that which naturally exists in the gastric juice without essentially impairing its digestive properties.

The remaining important ingredient of the gastric juice is its albuminoid matter, known under the name of *pepsine.* This substance is not precipitated by either the organic or the mineral acids, but is thrown down by the action of heat and by alcohol in excess. It may also be precipitated, like ptyaline, from its watery solution acidulated with dilute phosphoric acid, by the addition of lime water; the precipitated lime phosphate bringing down the pepsine entangled with it. Pepsine

[1] Annalen der Chemie und Pharmacie, 1854, p. 42.

[2] Bernard. Leçons de Physiologie Expérimentale. Paris, 1856, p. 396.

is not affected in the same way, however, by all the agents which cause its coagulation. After precipitation by alcohol or by lime phosphate, it is unchanged in its chemical qualities, and may be again dissolved in water without losing any of its original digestive properties; but when coagulated by boiling, it is permanently altered and cannot again be brought into an active condition.

Pepsine may also be precipitated from the gastric juice by contact with the *bile*. If ten to fifteen drops of dog's bile be added to 10 cubic centimetres of fresh gastric juice from the same animal, a complete precipitation takes place; so that the whole of the biliary coloring matter is thrown down as a deposit and the filtered fluid is found to have lost its digestive power although it still retains an acid reaction. This explains the disturbing effect upon digestion produced by a regurgitation of bile through the pylorus into the stomach.

Pepsine may be extracted from the fresh mucous membrane of the stomach by cutting it into small pieces and macerating it for some hours with distilled water. The filtered fluid, acidulated with dilute hydrochloric acid until it presents a similar grade of acid reaction to that of the fresh gastric juice, is found to possess the peculiar digestive properties of the natural secretion.

These digestive properties depend accordingly upon the presence of both the pepsine and the free acid. They are not exhibited by a dilute acid alone, nor by a solution of pepsine which is neutral or alkaline in reaction. The pepsine, which acts in some unexplained manner, like other so called "catalytic" bodies, requires, as a special condition of its activity, the presence of a free acid. Accordingly, the fluids of the stomach, even though they contain pepsine, will not act upon the food unless they have also an acid reaction. If the fresh gastric juice be neutralized by the addition of an alkali, it loses its digestive properties as soon as the point of neutralization is reached; but these properties may be restored by again acidulating the fluid. For this purpose, either lactic or hydrochloric acids may be used, both of which yield very active digestive fluids with pepsine. Dilute sulphuric, nitric, and acetic acids, on the other hand, according to Lehmann,[1] produce a mixture of only slight digestive power; while phosphoric, oxalic, and tartaric acids are nearly inert in this respect. If the gastric juice, again, be subjected to a boiling temperature, it is found to have lost its digestive properties owing to the chemical alteration of its pepsine, notwithstanding its acid reaction may remain the same as before.

The characteristic property of the fresh gastric juice, as well as of acidulated solutions of pepsine, is that it has the power of *digesting and dissolving substances of an albuminous nature.* This is best shown by suspending in gastric juice pieces of coagulated fibrine and keeping the fluid at the temperature of 38° (100° F.). The fibrine rapidly swells

[1] Physiological Chemistry. Cavendish Society edition. London, 1853, vol. ii. p. 58.

up, becomes transparent and gelatinous, and after a time dissolves. The same effect is produced, though more slowly, upon hard-boiled white of egg. The solid caseine of cheese is liquefied and the oleaginous particles set free. This action is in every case more or less dependent upon the temperature. It is entirely suspended at or near the freezing point, but becomes more and more active with the increase of warmth, and is most energetic from 35° to 40° (about 100° F.). Above that point its activity again diminishes, and at a boiling temperature it is entirely destroyed. It is owing to the influence of temperature that digestion is more slowly performed in the cold-blooded reptiles than in the warm-blooded birds and quadrupeds. This difference has been shown by Schiff,[1] who made acidulated infusions of the stomachs of two serpents, and placed in each the same measured quantity of coagulated albumen; one of the infusions being allowed to remain at a temperature varying from 10° to 17° (50° to 62° F.), the other being introduced, in a closed glass tube, into the stomach of a living dog. The second was found to have digested in six hours as much albumen as the first at the end of three weeks.

The changes produced in solid albuminous matters during digestion by gastric juice are as follows: The first effect is a swelling and gelatinization of the substance under the influence of the free acid. This will take place by the action of a dilute acid alone, and with the aid of continuous warmth a part of the substance will after a time even be dissolved. This solution, however, is not a true digestion of the albuminous body. It has merely been modified in such a way as to be soluble in an acidulated liquid, and it may be again precipitated by neutralizing the solution by means of an alkali or an alkaline carbonate. This modification of the albuminous matter, however, by the action of the free acid, seems to be an essential preliminary in the digestive act. If it be allowed to go on farther, the influence of the pepsine produces a more important change, by which the original substance is converted into *albuminose.* In this form it is no longer precipitable by neutralization of the fluid, and has consequently become soluble in water. It is not coagulable by boiling, either in a neutral, acid, or alkaline liquid; and it is not precipitable by nitric acid or by potassium ferrocyanide, although it may still be thrown down by alcohol in excess. It has thus become essentially altered in its chemical relations.

An equally or even more important change has also taken place in its physical characters; that is, it has acquired the property of *diffusibility.* The other liquid albuminous matters, as albumen, caseine, mucosine, and the like, do not pass through parchment paper or the substance of an animal membrane; or they pass, if at all, very slowly and in small quantity. Even pepsine is retained in this way almost completely by such a membrane. Albuminose, on the contrary, diffuses itself with great readiness through membranous partitions, and can be

[1] Lecons sur la Physiologie de la Digestion. Paris, 1867, tome ii. p. 19.

detected by its ordinary reactions in the external liquids. It is thus suited for absorption by the mucous membrane of the alimentary canal.

All the albuminous matters, without exception, which are susceptible of digestion, whether of animal or vegetable origin, are finally converted by the action of the gastric juice into albuminose. They therefore lose their original distinctive properties, and, when fully prepared for absorption into the bloodvessels, are all reduced to the condition of a single substance.

A further very remarkable peculiarity of the gastric juice is its aptitude for *resisting putrefaction.* While other animal fluids, as the saliva, the bile, the pancreatic juice, mucus and blood, enter into putrefaction with great readiness, the gastric juice remains when exposed to the air at ordinary temperatures for many months without developing any putrescent odor or losing its characteristic properties. It becomes somewhat darker in color, and after a time deposits a brownish sediment upon the bottom of the vessel, but it still retains its acid reaction and its power of digesting albuminous matters. Gastric juice will even arrest putrefactive changes when they have already begun in organic substances; and consequently putrefaction does not go on in the living stomach. Dr. Beaumont preserved some fragments of meat unaltered for a month in gastric juice, while other portions of the same substances, kept in saliva, were putrefied in ten days. Spallanzain found in the stomach of a viper the body of a lizard which had remained there for sixteen days without undergoing any putrefactive alteration; and similar observations have been made by other physiologists.

Mode of Secretion of the Gastric Juice.—As a rule, the gastric juice is not a constant but an occasional secretion, being poured out only when food is taken into the stomach. Dr. Beaumont found it to be entirely absent during the intervals of digestion, the stomach containing at that time no acid watery fluid, but only a little neutral or alkaline mucus. He was able to obtain a sufficient quantity of gastric juice for examination, by gently irritating the mucous membrane with a gum-elastic catheter, or the end of a glass rod, and by collecting the secretion as it ran in drops from the fistula; and on the introduction of food he found that the mucous membrane became turgid and reddened, a clear acid fluid collected everywhere in drops underneath the layer of mucus lining the walls of the stomach, and was soon poured out abundantly into its cavity. Prof. F. G. Smith, in his subsequent observations upon Alexis St. Martin, also found the fluids obtained from the empty stomach invariably neutral in reaction; while during digestion, whatever might be the nature of the food, they were always acid. Other observers, in experimenting upon the dog, have found more or less acid reaction always present at the surface of the mucous membrane. According to our own observations, the irritability of the gastric mucous membrane, and the readiness with which the flow of gastric juice may be excited, varies considerably in different animals, even in those belonging to the same species. In experimenting with gastric fistulæ on different dogs,

for example, we have found in one instance, like Dr. Beaumont, that the gastric juice was always entirely absent in the intervals of digestion; the mucous membrane then presenting invariably either a neutral or slightly alkaline reaction. In this animal, which was a perfectly healthy one, the secretion could not be excited by any artificial means, such as glass rods, metallic catheters, and the like; but only by the natural stimulus of ingested food. Tough and indigestible pieces of tendon, introduced through the fistula, were expelled again in a few minutes, one after the other, without exciting the flow of a single drop of acid fluid; while pieces of fresh meat, introduced in the same way, produced at once an abundant supply. In other instances, on the contrary, the introduction of metallic catheters or glass rods into the empty stomach has produced a scanty flow of gastric juice; and in experimenting upon dogs that have been kept without food during various periods of time and then killed by section of the medulla oblongata, we have usually, though not always, found the gastric mucous membrane to present a distinctly acid reaction, even after an abstinence of six, seven, or eight days. There is at no time, however, under these circumstances, any considerable amount of fluid present in the stomach; but only sufficient to moisten the gastric mucous membrane, and give it an acid reaction.

The gastric juice which is obtained by irritating the stomach with a metallic catheter is clear, perfectly colorless, and acid in reaction. A sufficient quantity of it cannot be obtained by this method for any extended experiments; and for that purpose, the animal should be fed, after a fast of twenty-four hours, with fresh lean meat, a little hardened by short boiling, in order to coagulate the fluids of the muscular tissue, and prevent their mixing with the gastric secretion. No effect is usually apparent within the first five minutes after the introduction of the food. At the end of that time the gastric juice begins to flow; at first slowly, and in drops. It is at first perfectly colorless, but soon acquires a slight amber tinge. It then begins to flow more freely, usually in drops, but often running for a few seconds in a continuous stream. In this way, from 60 to 75 cubic centimetres may be collected in the course of fifteen minutes. Afterward it becomes somewhat turbid with the debris of the food, which has begun to be disintegrated; but from this it may be readily separated by filtration. After three hours, it continues to run freely, but has become very much thickened, and even grumous in consistency, from the abundant admixture of alimentary debris. In six hours after the commencement of digestion it runs less freely, and in eight hours has become very scanty, though it continues to preserve the same physical appearances as before. It ceases to flow altogether in from nine to twelve hours, according to the quantity of food taken. For purposes of examination, the fluid drawn during the first fifteen minutes after feeding should be collected, and at once separated by filtration from accidental impurities. Obtained in this way it represents, as closely as possible, the normal constitution of the gastric juice as secreted by the stomach during the digestive process.

Both the essential constituents of the gastric juice, namely, the pepsine and the free acid, are produced by the glandular mucous membrane of the stomach. It would appear, however, that the mode of their production is somewhat different. Pepsine is an albuminoid substance formed by the nutritive process in the glands themselves. It probably accumulates in the intervals of digestion, and may therefore be extracted from the substance of the mucous membrane in the manner already described. On the other hand, the free acid appears in quantity only at the time of digestion, and is poured out with the watery constituents of the secretion. There is evidence, however, that the acid is not immediately formed by the glandular cells, but is produced by a subsequent, though very rapid, change after the fluid has been secreted. The acid reaction of the gastric fluids is never strongly pronounced in the deeper and middle parts of the mucous membrane, but only upon its free surface. This was shown by Bernard,[1] who injected into the jugular vein of a rabbit two successive solutions, one of iron lactate, the other of potassium ferrocyanide. These two salts would remain unaltered in neutral or alkaline fluids, but in the presence of a free acid would unite to form Prussian blue (iron ferrocyanide). On killing the animal three-quarters of an hour afterward, no blue coloration was found anywhere excepting in the stomach; and in this organ it was confined to the free surface of the mucous membrane, not being perceptible in the substance of the glands. As the two salts must have both exuded from the blood-vessels of the mucous membrane, it is evident that it was only at or near its upper surface that they met with a sufficient quantity of free acid to cause their combination. According to Dr. Lauder Brunton,[2] moreover, a horizontal section through the lower part of the gastric glands of the pigeon, if tested by litmus paper, will be found to have a neutral or extremely weak acid reaction, while the inner surface of the stomach presents a strongly marked acidity. At the same time, the deeper parts of the mucous membrane contain pepsine in sufficient quantity to form a digestive fluid, if extracted and acidulated in the usual way. Finally, the free acid continues to be formed during a certain time after death; for it has been found that if the fresh gastric mucous membrane of a rabbit or a pig be cut in small pieces and washed with distilled water until all trace of acidity is removed, it will again acquire an acid reaction after being left to itself for some hours. The materials of the free acid of the gastric juice are therefore furnished during life by the alkaline fluids of the circulating blood; but the acid itself originates subsequently by some change taking place in the products of exudation.

Self-digestion of the Stomach after Death.—Notwithstanding that the gastric juice has the power, at the temperature of the living body, of digesting all soft tissues composed of albuminous matter, yet owing to

[1] Liquides de l'Organisme. Paris, 1859, tom. ii. p. 375.

[2] Handbook for the Physiological Laboratory. Philadelphia, 1873, p. 491.

the mode of its production it does not attack the walls of the stomach itself. As the pepsine alone accumulates in any considerable quantity in the gastric follicles, while the acid ingredient appears abundantly only at the time of digestion, no dissolving action can be manifested while the organ is empty of food. It has already been seen, furthermore, that during the active secretion of the gastric juice, its free acid is formed by some modification in the exuded fluids, so that it is distinctly perceptible only in the fluids on the free surface and in the cavity of the stomach. In the substance of the mucous membrane, the acid fluid, even if absorbed, could not exert its solvent action, since it must be at once neutralized by the alkaline plasma of the circulating blood.

Even after death the gastric mucous membrane usually remains nearly intact, because, as a general rule, digestion has been at least partially suspended during the last hours of life, and the stomach accordingly contains little or no gastric juice. Still it is rare, in the human subject, to make an examination of the body twenty-four or thirty-six hours after death, without finding the mucous membrane in the great pouch of the stomach more or less softened and altered in its appearance from this cause. Sometimes, when death takes place suddenly, by violence or accident, in a healthy person, soon after the ingestion of food, and when the body has been protected against rapid cooling, the accumulated gastric juice acts powerfully upon the walls of the stomach as well as upon the food which it contains. Owing to the stoppage of the circulation, the local alkalescence of the fluids is no longer maintained, and the increasing quantity of free acid at last preponderates over the blood remaining in the capillary vessels. The mucous membrane becomes imbibed with an active digestive fluid, and in the course of ten or twelve hours may be thoroughly softened and disintegrated, exposing the submucous layer of connective tissue; and occasionally all the coats of the organ have been found destroyed, with a perforation leading into the peritoneal cavity. These changes show that, after death, the gastric juice, if present in sufficient quantity, may dissolve the coats of the stomach without difficulty; while during life, the changes of nutrition going on in the tissues protect them from its influence, and effectually preserve their integrity.

Daily Quantity of the Gastric Juice.—The quantity of gastric juice, secreted during a given time, like that of the saliva, varies very much according to the condition of the secreting organ. In many instances, as we have already seen, it is entirely absent during the intervals of digestion, and is poured out in abundance under the stimulus of recently introduced food. An exact estimate of the normal daily quantity is difficult for several reasons. First, it is evident that if the secretion be excited by artificial irritation of the gastric mucous membrane with insoluble glass or metallic substances, its quantity is not so abundant as when produced by the stimulus of natural food. Secondly, if excited by the introduction of food, a part of it is almost necessarily absorbed by the alimentary material, and consequently cannot be collected for

measurement; and thirdly, if we measure the quantity obtainable by either of these means during a short period, it does not follow that it would continue to be secreted at the same rate during the remainder of the twenty-four hours, because the rapidity of its production is so much influenced by the condition of the digestive process. Neither can we draw from an animal with a stomach fistula all the gastric juice which will flow during twenty-four hours, and consider that as representing the normal daily quantity; because we should then be drawing away a quantity of secreted fluid which in the natural condition is retained in the alimentary canal and reabsorbed by the bloodvessels. Its supply would therefore be necessarily diminished by the continuous loss of fluids from the system. Notwithstanding these difficulties, however, a sufficient number of facts have been observed to show that the usual daily secretion of the gastric juice is undoubtedly far more abundant than that of the other digestive fluids. Dr. Beaumont was able to obtain from the stomach of St. Martin, simply by the introduction of a gum-elastic catheter, 44 grammes of gastric juice in the course of fifteen minutes. We have often collected from a medium-sized dog, under the stimulus of commencing digestion, from 60 to 75 grammes in the same time. Bidder and Schmidt found that, in a dog weighing about 15.5 kilogrammes, they were able to obtain, by separate experiments, consuming in all twelve hours, 793 grammes of gastric juice. If these separate experiments, therefore, as is probable, indicate the average rate of its production at differents parts of the day, the entire quantity for twenty-four hours, in an animal of that size, would be 1586 grammes; or about 100 grammes for every kilogramme in weight of the body of the animal. By applying this calculation to a man of ordinary size the authors estimate the average daily quantity of gastric juice in the human subject as about 6500 grammes. It is, however, quite unsafe to estimate the quantity of this secretion as necessarily in proportion to the weight of the body. It is probably more strictly in proportion to the quantity of food which it is its function to digest; and the dog habitually consumes a much larger quantity of animal food, in proportion to his size, than a man. Schmidt, in the series of observations already quoted,[1] performed upon a woman with accidental gastric fistula, whose weight was only 53 kilogrammes, obtained, as the mean result of several observations, 580 grammes of gastric juice from the fistula in the course of an hour. In this case, however, the secretion was much poorer in its characteristic ingredients than that usually obtained from the dog, and was also much inferior in digestive power.

Another method which has been adopted for estimating the quantity of the gastric juice is to ascertain the amount capable of digesting the quantity of albuminous food required per day. According to the experiments of Lehmann,[2] one gramme of coagulated albumen, calculated as

[1] Annalen der Chemie und Pharmacie, 1854, Band xcii. p. 42.

[2] Physiological Chemistry. London, 1853, vol. ii. p. 53.

dry, requires for its solution 20 grammes of gastric juice. As the average daily consumption of albuminous matter in man is 130 grammes, this would accordingly require in him the secretion of 2600 grammes of gastric juice per day. Our own observations on the digestibility of fresh meat make the daily requirement still higher. A weighed quantity of fresh lean meat, containing 78 per cent. of water and 22 per cent. of solid ingredients, was cut into small pieces, and digested for ten hours, with frequent agitation, in a measured quantity of fresh gastric juice at the temperature of 38° (100° F.). At the end of that time, the liquefied portions were filtered away, the residue evaporated to dryness, and the quantity of fresh meat remaining undissolved thus calculated from the percentage of its solid ingredients. In this way it was found that one gramme of meat had been liquefied by 13.5 grammes of the digestive fluid; and accordingly the 453 grammes of meat consumed by a man in twenty-four hours would require for complete solution a little over 6000 grammes of gastric juice. This agrees very nearly with the estimate of Bidder and Schmidt given above. If the gastric juice were the only digestive fluid which acts on the food, we could rely fully on the foregoing estimate. But below the stomach other secretions also take part in the digestive process; and it is possible that some of them, especially the pancreatic juice, have also a certain amount of action upon albuminous matters, and may facilitate considerably their solution in the intestine. For the partial solution of meat, the disintegration of its fibres, and its reduction to a soft, grumous, liquid or semiliquid consistency, Dr. Beaumont found a much smaller quantity of gastric juice to be sufficient. In one experiment 1 gramme of cooked meat was completely disintegrated in this way by 2.5 grammes, and in another by 1.83 grammes of gastric juice. Its entire solution would of course have required a larger quantity.

These data are accordingly insufficient for determining the precise quantity of the secretion required for the digestive process. But if we allow sufficient weight to all the observations on this subject, it is evident that the gastric juice is very abundant; and it would not be an extravagant calculation to estimate its quantity as at least 3000 grammes per day.

Physiological Action of the Gastric Juice.—From the properties of the gastric juice already ascertained, it is seen to have an energetic action upon the albuminous ingredients of the food. As but few of the alimentary substances, however, habitually taken by either man or animals, consist solely of albuminous matter, the changes which they actully undergo in the stomach become a subject for further investigation.

The first effect of the introduction of food into the stomach, according to all observers, is an increased vascularity of its mucous membrane, a slight elevation of its temperature, and the immediate exudation, in more or less abundant quantity, of its acid secretion. At the same time the stimulus of the ingested food excites the *peristaltic movement*

of the stomach, which is accomplished by the alternate contraction and relaxation of the longitudinal and circular fibres of its muscular coat. The motion is minutely described by Dr. Beaumont, who examined it, both by watching the movements of the food through the gastric fistula, and also by introducing into the stomach the bulb and stem of a thermometer. According to his observations, when the food first passes into the stomach, and the secretion of the gastric juice commences, the muscular coat, which was before quiescent, is excited and begins to contract actively. The contraction takes place in such a manner that the food, after entering the cardiac orifice of the stomach, is first carried to the left into the great pouch of the organ, thence downward and along the great curvature to the pyloric portion. At a short distance from the pylorus, Dr. B. often found a circular constriction of the gastric parietes, by which the bulb of the thermometer was gently grasped and drawn toward the pylorus, at the same time giving a twisting motion to the stem of the instrument, by which it was rotated in his fingers. In a moment or two, this constriction was relaxed, and the bulb of the thermometer again released and carried, together with the food, along the small curvature of the organ to its cardiac extremity. This circuit was repeated so long as any food remained in the stomach; but, as the liquefied portions were successively removed toward the end of digestion, it became less active, and at last ceased altogether when the stomach had become completely empty, and the organ returned to its ordinary quiescent condition.

It is easy to observe the muscular action of the stomach during digestion in the dog, by the assistance of a gastric fistula, artificially established. If a metallic catheter be introduced through the fistula when the stomach is empty, it must usually be held carefully in place, or it will fall out by its own weight. But immediately upon the introduction of food, it can be felt that the catheter is grasped and retained with some force, by the contraction of the muscular coat. A twisting or rotatory motion of its extremity may also be frequently observed, similar to that described by Dr. Beaumont. This peristaltic action of the stomach, however, is a gentle one, and not at all active or violent in character. We have never seen, in opening the abdomen, any such energetic or extensive contractions of the stomach, even when full of food, as may be easily excited in the small intestine by the mere contact of the atmosphere, or by pinching with the blades of a forceps. This difference in activity between the peristaltic movement of the stomach and that of the intestine corresponds to the difference in its object and result. In the intestine the peristaltic action carries the semifluid contents of the alimentary canal continuously from above downward; in the stomach it produces a kneading effect upon the masticated food, and mixes it intimately with the gastric juice. This action of the stomach, accordingly, though quite gentle, is sufficient to produce a constant churning movement of the food, by which it is carried back and forward to every part of the stomach, and incorporated with

the gastric juice, which is at the same time poured out by the mucous membrane; so that the digestive fluid is made to penetrate equally every part of the alimentary mass, and the digestion of all its albuminous ingredients goes on simultaneously. This movement of the stomach is one which cannot be completely imitated in experiments on artificial digestion with gastric juice in test-tubes; and consequently the process, under these circumstances, is never so rapid as when it takes place in the interior of the stomach.

The result of the action of the gastric juice, thus incorporated in the stomach with the alimentary matters, is that they are *disintegrated by the softening and liquefaction of their albuminous ingredients.* Bread consists mainly of hydrated starch, entangled and incorporated with the semi-solid gluten. By digestion in the stomach, the gluten is digested and liquefied by its conversion into albuminose, the starch being thus set free, and the whole reduced to a diffluent condition. The same effect can be seen when bread is subjected to the action of gastric juice in a test-tube, the gluten passing into the condition of liquid albuminose, while a deposit of unaltered starch settles at the bottom. Cheese, consisting of coagulated caseine and milk globules, undergoes an analogous change. Its caseine is liquefied by digestion, while its liberated fat globules rise to the upper part of the fluid, forming a creamy-looking layer upon its surface.

Adipose tissue is very readily disintegrated by the liquefaction of its connective tissue, which is formed of albuminous matter, while the fatty matter escapes in the form of oil drops, floating upon the surface of the other contents of the stomach. Dr. Beaumont always found free fat, in the form of oil globules, thus extricated from the fatty tissues soon after they had been introduced into the stomach with the food; and it is easy to verify this observation, either by artificial digestion of adipose tissue in gastric juice, or by opening the stomach of an animal soon after the administration of food containing fat.

The digestion of *muscular flesh* is also at first a process of disintegration. The connective tissue intervening between the fibrous bundles yields to the action of the gastric juice, and the fibres themselves thus become separated from each other, and form a gruelly mixture of minute and almost microscopic threads and fragments. The substance of the muscular fibres then also begins to become altered—they break up into shorter fragments, and, when examined by the microscope, are found to have lost the distinctness of their transverse striations. If the food have been thoroughly masticated before being taken into the stomach, this change goes on rapidly and uniformly throughout the mass. If, as in the dog, the meat be swallowed without much mastication, or if portions be suspended in a test tube containing gastric juice, the action progresses regularly from without inward. The external parts of the muscular tissue are first softened and decolorized, and become covered with a grayish layer, of grumous consistency, containing the isolated and partially destroyed fragments of muscular fibre. As these por-

tions are removed by the peristaltic movements of the stomach, the digestive action extends to the parts underneath, and so on until the whole has been reduced to a uniform mixture, of a thickish gruelly consistency, in which the distinctive elements of the tissue are no longer recognizable by the eye, and in which the remnants of the muscular fibres can only be detected by the microscope. It is this apparently homogeneous, pultaceous or gruelly semi-fluid material that was formerly designated by the name of "Chyme." It is evidently nothing more than a mixture of the disintegrated remnants of the digested tissues, portions of which have been completely liquefied while others are not yet reduced to a state of solution.

When *milk* is taken into the stomach in a fresh condition, its caseine is at first coagulated, afterward dissolved. The preliminary coagulation, which is due to the action of the pepsine and dilute acid, takes place very rapidly. Dr. Beaumont found that milk could be withdrawn in a coagulated condition in fifteen minutes after its introduction into the stomach; and that if the mixture were kept at the temperature of 38° (100° F.), the coagula were again liquefied in the course of eight hours. The coagulation of milk, thus produced by its first contact with the gastric juice is, however, no obstacle to its subsequent digestion. The caseine does not form a solid uniform clot, but is thrown down in the form of minute flocculi, of soft consistency, which are constantly bathed by the digestive fluids, and at the temperature of the living body undergo readily the conversion into albuminose. As it is this chemical change which constitutes the real process of digestion, the preliminary coagulation of the caseine does not interfere with its accomplishment. Milk, furthermore, as used by adults, is to a large extent incorporated, in the coagulated form, with other solid or semi-solid articles of food.

The substance of *vegetable tissues*, as a rule, is digested in a similar manner to that described above. The albuminous matters are dissolved out, leaving the starchy or oleaginous ingredients in a free condition, but chemically unchanged. As these tissues generally contain a much smaller proportion of albuminous matter than most kinds of animal food, their disintegration is the main result of the changes which they undergo in the stomach.

The gastric juice, together with the disintegrated debris of the food, after commencing its action in the stomach, *passes into the upper part of the intestine.* This can be seen readily in the dog by killing the animal after feeding, and examining the contents of the intestine. We have observed the same thing by establishing, in the dog, an artificial duodenal fistula, by means of an operation similar to that for producing a permanent fistula of the stomach. A silver tube, armed at each end with narrow projecting flanges, is introduced into the lower part of the duodenum, and the wound allowed to heal, after which the contents of the intestine may be withdrawn at will, and subjected to examination at different periods during digestion.

By examining in this way, from time to time, the intestinal fluids, it becomes manifest that the action of the gastric juice, in the digestion of albuminous substances, is not confined to the stomach, but continues after the food has passed into the intestine. About half an hour after the ingestion of a meal, the gastric juice begins to pass into the duodenum, where it may be recognized by its strongly-marked acidity, and by its peculiar action, already described, in interfering with Trommer's test for glucose. It has accordingly already dissolved some of the ingredients of the food, and contains a certain quantity of albuminose in solution. It soon afterward, as it continues to pass into the duodenum, becomes mingled with the debris of muscular fibres, fat vesicles, and oil drops; substances which are easily recognizable under the microscope, and which produce a grayish turbidity in the fluid withdrawn from the fistula. By the continuous passage, in this way, of the alimentary material, mixed with gastric juice, through the pylorus into the intestine, the stomach becomes gradually cleared of its contents. According to Dr. Beaumont the time required for the entire disappearance of food from the stomach varies from one hour to five hours and a half, according to the quality and quantity of the material used. In the experiments of Prof. Francis G. Smith upon the same subject, food seldom remained in the stomach more than two hours after its introduction. Three hours is probably sufficient, as a rule, for the completion of stomach digestion, in the human subject, when the food is in moderate quantity and has been properly prepared by cooking and mastication. In the carnivorous animals generally, where the food is swallowed in fragments of some size, the process is longer; and in the dog a moderate meal of fresh uncooked meat requires from nine to twelve hours for its complete liquefaction and disappearance from the stomach.

The gastric juice, after having accomplished its work in the digestion of the food, is *reabsorbed* from the alimentary canal and taken up by the bloodvessels. It thus forms a vehicle for the dissolved nutritious materials, and again enters the circulation with the alimentary substances which it holds in solution. It is in this way that the system is enabled to furnish so abundant a secretion without being exhausted by drainage. The reabsorption of the gastric juice goes on simultaneously with its secretion during the continuance of the digestive act; and the fluids which the blood loses by one process are incessantly restored to it by the other. An abundant supply, therefore, of the secretion may be poured out during the digestion of a meal, at an expense to the blood, at any one time, of only a small quantity of fluid. The simplest investigation shows that the gastric juice does not accumulate in the stomach to any considerable amount during digestion; but that it is gradually secreted so long as any food remains undissolved; each portion, as it is digested, being disposed of by reabsorption, together with its solvent fluid. There is accordingly, during digestion, a continuous circulation of the digestive fluids from the bloodvessels to

the alimentary canal, and from the alimentary canal back again to the bloodvessels.

That this circulation really takes place is shown by the following facts: First, if a dog be killed some hours after feeding, there is never more than a very small quantity of fluid found in the stomach, just sufficient to smear over and penetrate the half digested pieces of meat; and secondly, in the living animal, gastric juice, drawn from the fistula five or six hours after digestion has been going on, contains little or no more albuminous matter in solution than that extracted fifteen to thirty minutes after the introduction of food. It has evidently been freshly secreted; and, in order to obtain gastric juice saturated with alimentary matter, it must be artificially digested with food in test-tubes, where this constant absorption and renovation cannot take place.

The secretion of the gastric juice is much influenced by nervous conditions. It was noticed by Dr. Beaumont, in his experiments upon St. Martin, that irritation of the temper, and other moral causes, would frequently diminish or altogether suspend the supply of the gastric fluids. Any febrile action in the system, or any unusual fatigue, was liable to exert a similar effect. Every one is aware how readily any mental disturbance, such as anxiety, anger, or vexation, will take away the appetite and interfere with digestion. Any nervous impression of this kind, occurring at the *commencement* of digestion, seems moreover to produce some change which has a lasting effect upon the process; for it is often noticed that when any annoyance, hurry, or anxiety occurs soon after the food has been taken, though it may last only for a few moments, the digestive process is not only liable to be suspended for the time, but to be permanently disturbed during the entire day. In order that digestion, therefore, may go on properly in the stomach, food must be taken only when the appetite demands it; it should be thoroughly masticated at the outset; and, finally, both mind and body, particularly during the commencement of the process, should be free from any unusual or disagreeable excitement.

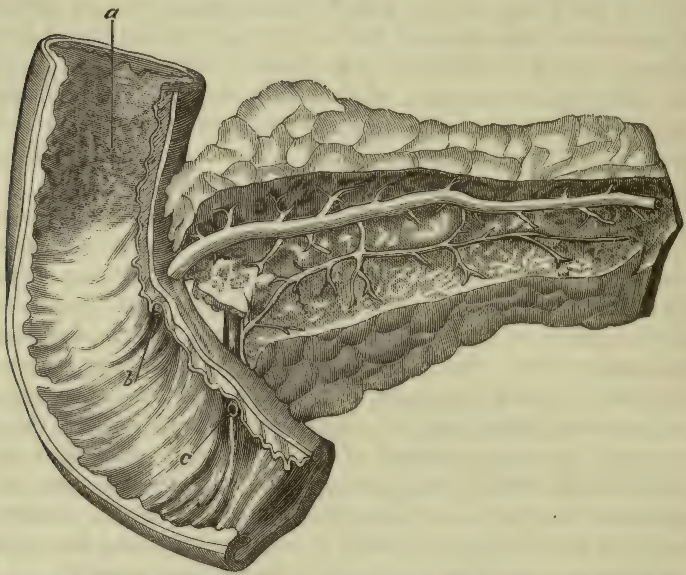
The Pancreatic Juice and its Action upon the Food.

The pancreas, which is a lobulated gland, similar in its general structure to the salivary glands, lies across the upper part of the abdomen in such a manner that its larger or right-hand extremity is in contact with the duodenum. It is traversed in its longitudinal direction by its main excretory duct, which receives, as it passes from left to right, the lateral branches coming from the glandular lobules, and finally, in the human subject, opens into the cavity of the duodenum, closely adjacent to the situation of the common biliary duct, at about ten centimetres below the pyloric orifice of the stomach. Its secretion thus enters the intestine, and mingles with the substances undergoing digestion, almost immediately after they have passed from the stomach into the duodenum.

The arrangement of the gland and its duct is similar to the above, in

its essential particulars, in most of the lower animals. In the dog and cat, there are two ducts opening into the intestine, one of them in juxtaposition with the orifice of the biliary duct, the other from one to three centimetres farther down. The lower of these ducts is usually, though

Fig. 46.



PORTION OF HUMAN PANCREAS AND DUODENUM.—*a*. Cavity of duodenum. *b*. Orifice of the pancreatic duct. *c*. Orifice of lower pancreatic duct. (Bernard.)

not always, the larger of the two, and they generally communicate with each other by a transverse branch, in the substance of the gland, before opening into the intestine. Even in the human subject, as shown by Bernard, Kölliker, and Sappey, there is often a smaller accessory duct opening into the intestine, sometimes above and sometimes below the situation of the principal one. The most marked peculiarity in the arrangement of the parts is seen in the rabbit, where the pancreatic duct is single, but opens into the intestine at a distance of from 30 to 40 centimetres below the orifice of the biliary duct.

The pancreatic juice has been obtained in many instances from the living animal by opening the abdomen during the act of digestion, and inserting a silver canula into the principal pancreatic duct, immediately before its entrance into the intestine. The canula being secured in its position by a ligature placed round the duct, the parts are returned into the abdominal cavity, and the external wound closed with sutures, leaving the open extremity of the canula projecting between its edges. The secretion is thus diverted from the intestine, and may be collected for examination as it flows from the canula. This operation has been done most frequently upon the dog, but also upon the rabbit, the ox,

the sheep, the goat, the pig, and the goose. The secretion has also been obtained from the horse, by opening the duodenum and inserting the canula into the natural orifice of the pancreatic duct.

Under these circumstances, the fistula produced is only a temporary one; since the ligature soon cuts its way through the duct by ulceration, when the canula falls out and the wound closes spontaneously, the natural communication of the duct with the intestine being at the same time re-established. Even in the ox, Colin found that the canula became displaced within six or eight days after the operation; and in the dog, according to Bernard, the same thing happens at the end of two or three days. Furthermore, the pancreas being very sensitive to external irritation, its secretion is liable to become altered in character during the inflammatory process, and it is therefore to be collected for examination only within the first twenty-four hours after the insertion of the canula.

A permanent pancreatic fistula has been successfully established by Ludwig and Bernstein, by making an incision in the side of the pancreatic duct near the intestine, introducing into the orifice thus made a leaden wire extending a short distance each way, toward the gland and toward the duodenum, and provided with an arm projecting at right angles from its middle, which is allowed to protrude from the external wound. After the healing of the parts, the fistula is thus kept permanently open by the wire, which lies somewhat loosely in the cavity of the duct and allows the secretion to escape by its side. The objection to the plan is that, as the secretion passes by a narrow fistulous passage, it may be mingled with unnatural secretions.

Physical Character and Composition of the Pancreatic Juice.—The pancreatic juice obtained from the dog within the first day after the introduction of the canula, and while digestion is going on, is a clear colorless fluid, with a distinctly alkaline reaction. It has a well marked viscidity, somewhat like that of the serum of blood, or uncoagulated white of egg, and differs strongly in this respect from the watery consistency of the gastric juice. It coagulates completely by the application of a boiling temperature, often solidifying into a uniform jelly-like mass. It also gelatinizes partially on being cooled down to the zero point (32° F.). According to the analyses of Schmidt,[1] it has the following composition:

COMPOSITION OF PANCREATIC JUICE.

Water	900.76
Pancreatine	90.44
Sodium chloride	7.35
Potassium chloride	0.02
Lime phosphate	0.41
Magnesium phosphate	0.12
Soda, lime, and magnesia, in combination with the pancreatine	0.90
	1000.00

[1] Annalen der Chemie und Pharmacie, 1854, xcii. p. 33.

The most important ingredient of the pancreatic juice is its animal matter, known as *pancreatine.* It is this substance which gives to the fluid its tenacious or viscid character, and, in the secretion obtained by the above method, it amounts to over ten per cent. of the whole, being more abundant than all the other solids taken together. It is also considerably more abundant, in proportion, than the albuminous ingredient of any other of the digestive fluids. It is coagulable by heat, by nitric acid, by alcohol, and also by magnesium sulphate added in excess. In this last particular it differs from albumen, which is not affected by magnesium sulphate. Another peculiarity, in which it resembles pepsine, is that after being precipitated by alcohol, it may be again dissolved in water, retaining all its original properties. By some observers it is considered as a mixture of several substances which differ from each other in their chemical relations; but, taken as a whole, it forms a strongly marked distinguishing ingredient of the pancreatic juice.

When drawn from the canula several days after its introduction, or obtained by means of a permanent fistula, the secretion is usually more abundant, but poorer in its organic constituents. Schmidt found that in the dog, immediately after the operation, the pancreatic juice was of a thick, tenacious consistency, containing an abundance of solid ingredients, consisting principally of organic matter; while that obtained from a permanent fistula was comparatively thin and watery, containing only from 1.5 to 3.6 per cent. of solids, of which not more than two-thirds consisted of organic matter. Other observers have met with the same difference. The fluid obtained soon after the introduction of the canula, during the period of digestion, probably represents most fully the normal secretion.

The organic matter of pancreatic juice, like that of the other digestive secretions, may be extracted from the substance of the glandular tissue. For this purpose the pancreas is taken out from the dog or pig, killed while digestion is going on, a few hours after the ingestion of food, cut into small pieces, or ground to a pulp with sand, and allowed to macerate for two hours in water at 25° (77° F.). The filtered fluid contains a substance nearly or quite identical in its properties with that contained in the pancreatic juice itself. It may also be obtained, in a form better adapted for permanent use, by placing the freshly divided pancreas for twenty-four hours in absolute alcohol, then separating it from the alcohol, and macerating it for several days in glycerine, which is afterward filtered. The glycerine extracts the organic matter of the glandular tissue, and preserves it without alteration. It may be precipitated at any time from the glycerine solution by the addition of strong alcohol, and afterward dissolved in water. It thus forms a watery extract of the pancreas.

Physiological Properties of the Pancreatic Juice.—This secretion has certain well marked characters which indicate that its action is of

great importance in the digestive process, although the precise limits of its operation are not yet fully determined.

In the first place, the pancreatic juice has the power of *transforming starch into sugar.* This action takes place with great rapidity at the temperature of the living body. According to Hardy,[1] it is much more prompt as well as more complete than the corresponding change produced by saliva, being at the temperature of 40° (104° F.) almost instantaneous; and, while the transforming action of saliva is very partial, much of the starch remaining unchanged, that of the pancreatic juice appears to convert the whole of it into glucose. Kroeger found[2] that one gramme of fresh pancreatic juice, at the temperature of 35° (95° F.), transformed into sugar, within thirty minutes, 4.67 grammes of starch; while, according to our own observations, if one gramme of fresh human saliva be mixed at 38° (100° F.), with a watery solution containing less than 0.1 gramme of boiled starch, though the sugar reaction becomes manifest in one minute, a large portion of the starch is still unchanged at the end of an hour. It is certain that hydrated starch, although it may be recognized for a long time in the stomach by its iodine reaction, disappears completely as soon as it enters the upper part of the duodenum. According to Ranke,[3] pancreatic juice causes the transformation not only of hydrated, but also of raw starch; a property which was found by Bouchardat and Sandras to be very energetic in the secretion of the common fowl, if aided by a slight elevation of temperature.

The organic matter of the pancreatic juice, which produces this change, is coagulable by a boiling temperature, and after its solution has once been boiled, it is inactive in regard to starchy matters. It is produced in the substance of the gland, probably by the transformation of some previously formed material, since it has been found by Liversidge,[4] that after it has been completely extracted from the chopped glandular tissue by treatment with glycerine, if the inactive residue be transferred to a filter, and allowed to remain exposed to the air for five or six hours, it is regenerated, and may be again extracted by the addition of water or glycerine. This is undoubtedly due to a real reproduction of the active organic substance, and is not the result of a putrefactive change, since the same observer found that a watery extract of the pancreas, which had once been deprived of its action on starch by boiling, never regained this property at any stage of subsequent decomposition.

Secondly, the pancreatic juice has the power of *emulsifying the fats.* This is perhaps its most marked and peculiar property, by which it is

[1] Chimie Biologique. Paris, 1871, p. 152.

[2] Cited in Milne Edwards, Leçons sur la Physiologie. Paris, 1862, tome vii. p. 68.

[3] Physiologie des Menschens. Leipzig, 1872, p. 271.

[4] Studies from the Physiological Laboratory of the University of Cambridge, Part I. Cambridge, 1873, p. 49.

especially distinguished from the other digestive secretions. If a fluid fatty substance, such as olive oil or melted butter, be shaken up in a test-tube with the saliva, the gastric juice, the bile, or any of the excreted fluids, it suffers no change in its physical characters. It is partially broken up by the mechanical agitation, but, on being allowed to remain at rest, the oil globules run together and soon collect in a distinct layer upon the surface of the liquid. If, on the contrary, the same experiment be tried with fresh pancreatic juice, the oil is instantly broken up into a state of fine subdivision, producing a uniformly white, opaque, milky looking fluid. The emulsion thus formed is permanent, the microscopic fat granules being held in suspension by the organic matter of the secretion, and thus prevented from uniting into visible oil drops. If the proportion of oily matter be considerable, a part of it may rise to the surface as a creamy layer, and if it be in excess, the superfluous portion will also rise to the upper part of the liquid; but the remainder will continue indefinitely in the emulsioned condition, disseminated uniformly through the fluid mixture.

The emulsifying property of the pancreatic juice is very active, when the secretion exhibits its normal characters. Bernard found that the freshly extracted juice formed a complete emulsion at 38° (100° F.) with olive oil, butter, suet, or lard, when mixed with either of these substances in the proportion of one gramme of oleaginous matter to two grammes of pancreatic juice. The emulsion thus produced retained its physical appearance unchanged, although allowed to remain at the above temperature for fifteen or eighteen hours.

The power of the pancreatic juice to emulsify oils, though facilitated by its alkaline reaction, does not depend upon the free alkali, but is mainly due to the action of its organic matter. This is indicated by the fact that other animal fluids which are also alkaline do not have the same power in a corresponding degree; and Bernard has shown that the pancreatic juice, after being neutralized by a dilute acid, still retains its property of acting upon the fats.

The property of emulsifying oily matters, first shown to exist in the pancreatic juice of the dog, has been found by Colin in that of the horse, the ass, the ox, the sheep, and the pig; and by Bernard has been found fully developed in that of the goose. According to Colin, its intensity, in these different animals, is proportional to the quantity of albuminous matter contained in the secretion; one part of oil requiring, for complete emulsion, from two to three parts of pancreatic juice when its albuminous ingredient is abundant, and four, five, or six parts when the proportion of this substance is diminished.

There is every evidence that the emulsifying action of the pancreatic juice is of the first importance in the digestion of fatty substances. These substances are not affected by contact with gastric juice outside the body; and examination shows that they are not digested in the stomach, but are unchanged in their essential character so long as they remain in the gastric cavity. They are merely melted by the warmth

of the organ, and set free by the solution of the vesicles, fibres, or capillary tubes in which they are contained, or among which they are entangled; and they are still readily discernible, floating in larger or smaller drops on the surface of the semi-fluid alimentary mass. Very soon, however, after its entrance into the intestine, the oily portion of the food loses its characteristic appearance, and is converted into a white, opaque emulsion, which is gradually absorbed. This emulsion is termed the *chyle*, and is always found in the small intestine during the digestion of fat, entangled among the valvulæ conniventes, and adhering to the surface of the villi. The digestion of fatty substances accordingly consists mainly in their emulsion, by which they are converted into chyle and made ready for absorption. This change begins to take place in the duodenum, immediately below the orifice of the pancreatic duct. But as the pancreatic and biliary ducts in most animals open into the intestine in company or in close juxtaposition with each other, it might, from this circumstance alone, be doubtful whether the two secretions have not an equal share in producing the effect. Bernard first removed the doubt by examining the products of digestion in the rabbit. In this animal, the biliary duct opens, in the usual manner, just below the pylorus, while the pancreatic duct, as stated above, communicates separately with the intestine 30 or 40 centimetres farther down; so that there is here a considerable extent of the small intestine already containing bile, but into which the pancreatic juice has not yet been discharged. Bernard fed these animals with substances containing oil, or injected melted butter into the stomach; and, on killing them afterward, found that there was no chyle in the intestine between the openings of the biliary and pancreatic ducts, but that it was abundant immediately below the orifice of the latter. Above this point, also, he found the lacteals empty or transparent, while below it they were full of white, opaque chyle. These experiments, which were confirmed by Prof. Samuel Jackson,[1] fully demonstrate that the emulsifying action of the pancreatic juice upon oily matters is exerted within the body during digestion, and is the direct agent in the production of chyle in the intestine.

Thirdly, the pancreatic juice at the temperature of the living body gradually *dissolves coagulated albuminous matters.* This property of the secretion, first recognized by Bernard and Corvisart, has been alternately confirmed and denied by various subsequent observers. Among those who found in the pancreatic juice more or less power of this kind, some stated it to be only present when the fluid was acidulated (Meissner), while others maintained that it could only be exerted in presence of an alkaline reaction (Wundt); and the information obtained in regard to the process has been generally much less distinct and satisfactory than that relating to the other properties of the secretion. The most definite

[1] American Journal of the Medical Sciences. Philadelphia, October, 1854.

and valuable observations on this subject are those of Kühne,[1] who experimented both with the pancreatic juice of the dog, and also with infusions of the glandular tissue. He found that the fresh viscid secretion could, in from half an hour to three hours, effect the solution of coagulated fibrine and albumen, without any modification of its alkaline reaction, and without giving rise to signs of putrefaction; the albuminous matters, thus dissolved, being changed into a substance not coagulable by boiling and readily diffusible through parchment paper. The product of this action accordingly resembles that obtained from a similar digestion with the pepsine of gastric juice.

In his experiments with the glandular tissue, Kühne placed the finely divided gland in warm water together with a weighed quantity of the substance to be experimented on; allowing the infusion of the pancreas and the digestion of the albuminous matter to proceed simultaneously. He found that when employing for this purpose a dog's pancreas of from 50 to 60 grammes weight, 400 grammes of boiled and pressed fibrine, after remaining in the infusion at 40° to 45° (104° to 113° F.) for from three to six hours, were reduced to an insignificant residue, the reaction of the mass continuing throughout faintly alkaline.

The details of this process, however, are different in some respects from those of digestion in gastric juice. If bits of coagulated fibrine be placed in gastric juice, or an acidulated solution of pepsine, they first swell up and become transparent under the influence of the free acid; and this action is preliminary to their subsequent solution and transformation into albuminose. But in an infusion of the pancreas, according to Kühne, the pieces of fibrine do not become at all swollen or altered in transparency, even when considerably softened and near the point of solution. They are, however, essentially modified in their physical and chemical properties. Boiled fibrine, by itself, is but slowly affected by dilute acids or alkalies, and is nearly or quite insoluble in a ten per cent. solution of hydrochloric acid; but after remaining for a time in an infusion of the pancreas, a part of it is found to be almost instantly soluble in a solution of hydrochloric acid of one part per thousand.

It is evident, accordingly, that the organic matter of the pancreatic juice may exert a transforming action on the albuminous matters, somewhat analogous to that of the pepsine of gastric juice. How far this action takes place in the natural process of digestion has not been demonstrated by direct observation, but it is possible that the two secretions may be in some degree complementary to each other. In the gastric juice, we have an abundant fluid with an acid reaction, and with a small proportion of organic substance; in the pancreatic juice a comparatively scanty secretion, but with a much larger proportion of organic matter, capable of exerting a transforming power on the albuminous ingredients of the food. While the gastric juice acts alone in the stomach, softening and disintegrating the food, and actually dissolving

[1] Archiv für Pathologische Anatomie und Physiologie, 1867, xxxix. p. 130.

a part of it; in the intestine the two secretions may act together, to complete the liquefaction of the alimentary materials.

Mode of Secretion and Daily Quantity of the Pancreatic Juice.—If examined in the living animal by means of a canula introduced into its excretory duct, it is found that the action of the pancreas is by no means the same at different times. If there be no food in the stomach or intestine, or if the process of digestion be arrested from any cause, no fluid whatever is discharged from the canula. If digestion be going on, the pancreatic juice soon begins to run from the orifice of the tube, at first slowly and in successive drops. Sometimes the drops follow each other with rapidity for a few moments, and then an interval occurs during which the secretion seems entirely suspended. After a time it recommences, and continues to exhibit similar fluctuations during the whole course of the experiment. Its flow, however, is at all times scanty, as compared with that of the gastric juice. We have never been able to collect, in a good sized dog, more than 75 grammes in the course of three hours, and usually the quantity was much less than this. Colin found a great variation in the animals upon which he experimented, the quantity being from two and a half to thirty times as abundant at one period as at another. In the bullock, the largest quantity obtained was 342 grammes per hour while the animal was engaged in rumination.

The entire quantity of pancreatic juice secreted per day cannot be determined with precision, but it is evidently moderate in amount, as compared with the other digestive fluids. In the ox, cow, and horse, Colin found the average quantity nearly the same, corresponding to about 0.58 gramme per hour for every kilogramme of the animal's weight. Schmidt, in his experiments upon the dog, found it, in recently established fistulæ, not more than 0.2 gramme per kilogramme per hour. In the most successful instances, we have found it in the dog, as much as 1.25 grammes per kilogramme per hour during active digestion, but much less than this in the intervals. If we take, as the average of these estimates, 0.5 gramme per hour for every kilogramme of bodily weight, it would give for a man of medium size about 800 grammes as the entire quantity of pancreatic juice secreted per day.

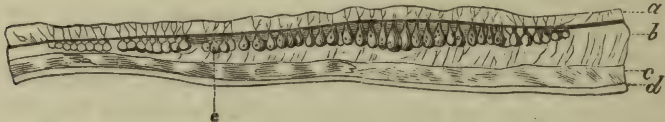
The condition of the pancreas varies at different periods corresponding with the activity of its secretion. In the intervals of digestion it is comparatively pallid and dense; during digestion it becomes turgid and vascular, its ruddy color showing the increased quantity of blood circulating in its vessels. According to most observers, the substance which is efficient in the solution of albuminous matters can only be extracted from the pancreas at this time, during the height of its vascularity and digestive action, which, in the dog, is from five to seven hours after the ingestion of food. When the process of digestion is terminated, its vascularity again diminishes, and the organ returns to its quiescent condition. This periodical excitement during the period of functional activity, though well marked in the pancreas, is not peculiar to it, but may also be seen in the mucous membrane of the stomach and the small

intestine. It probably exists, more or less fully developed, in all the organs taking part in the digestive process.

The Intestinal Juice and Digestion in the Intestine.

The secretory apparatus of the small intestine consists of two sets of glandular organs, namely, first, *Brunner's glands*, which are compound or lobulated, and confined to the upper part of the duodenum, forming a sort of collar round the intestine for a distance of several centimetres from the pylorus; and, secondly, the *follicles of Lieberkühn*, which are simple tubular glandules, occupying the substance of the mucous membrane for the whole length of the small intestine.

Fig. 47.



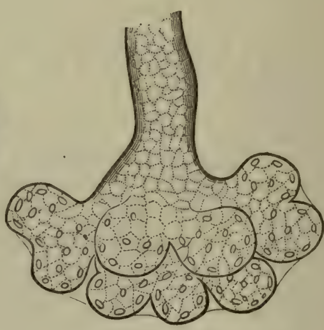
LONGITUDINAL SECTION OF WALL OF DUODENUM IN THE DOG; showing the submucous layer of Brunner's Glands. *a.* Mucous membrane. *b.* Layer of submucous connective tissue, in which the glands are situated. *c.* Muscular coat. *d.* Peritoneal coat. *e.* Brunner's glands, with their ducts opening upon the free surface of the mucous membrane. (Bernard.)

Brunner's glands, or the duodenal glandules as they are sometimes called, are situated in the submucous layer of connective tissue in this part of the intestine. They are spherical, or, when thickly set, irregularly flattened or polygonal in shape from mutual pressure, and from $\frac{1}{2}$ to 1 millimetre in diameter.

Fig. 48.

Entire BRUNNER'S GLAND, from human intestine. (Frey.)

Fig. 49.



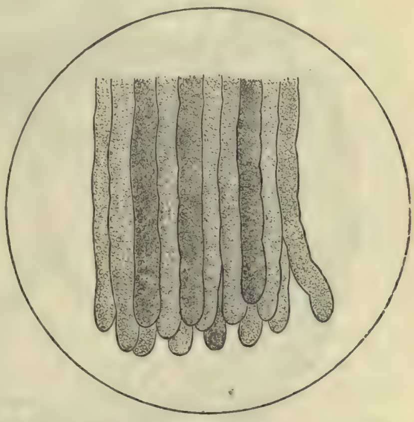
Portion of one of BRUNNER'S GLANDS, from human intestine.

In their structure, the glands are similar to the lobulated glandules of the mouth, being composed of rounded follicles clustered about a central branching excretory duct. Each follicle is about $\frac{1}{10}$ of a millimetre in diameter, and consists of a delicate membranous wall, lined

with cells of glandular epithelium, showing small but distinctly marked nuclei. The follicles collected round each terminal branch of the main duct are bound together by a thin layer of connective tissue, and covered with a plexus of capillary bloodvessels.

The follicles of Lieberkühn, which are much more numerous than the preceding, are not situated in the submucous connective tissue, but occupy the entire thickness of the mucous membrane, forming, like the gastric follicles in the mucous membrane of the stomach, the greater part of its substance. They are simple, nearly straight tubules, from $\frac{1}{12}$ to $\frac{1}{16}$ of a millimetre in diameter, lined throughout with cylindrical epithelium, opening by their orifices upon the free surface of the intestinal mucous membrane and terminating below by rounded extremities. They are so thickly set that in many places there appears to be no space left between them, except that occupied by the capillary bloodvessels which encircle them in every direction.

Fig. 50.



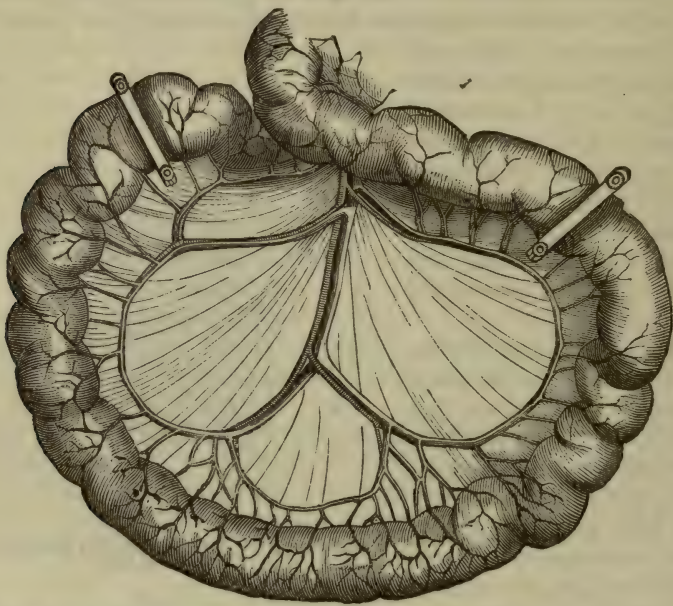
FOLLICLES OF LIEBERKUHN, from Small Intestine of Dog.

The fluid produced by the mucous membrane of the small intestine consists of a mixture of the secretions of these two sets of glands. But as, owing to the situation of Brunner's glands, it has been found impossible to obtain their secretion unmixed with other fluids, and as it is evidently much less abundant than that produced in the remainder of the intestine, the secretion of the follicles of Lieberkühn is regarded as the main constituent of the intestinal juice. It is by no means easy to obtain this fluid in a pure form and in normal condition. There is no single excretory duct, like that of the pancreas, into which a canula might be inserted; and a fistulous opening made in the intestine itself would of course yield a mixture of all the secretions discharged into its cavity. If these should be shut off by a ligature permanently applied above the fistula, the disturbance of the digestive process would be so great, that the experiment could hardly be expected to give a valuable result.

Nevertheless, attempts have been made, by various methods, to obtain the intestinal juice in condition sufficiently pure for examination. Bidder and Schmidt first tied the biliary and pancreatic ducts, and then established an intestinal fistula below, from which they extracted the fluids accumulated in the cavity of the gut. Frerichs operated by opening the abdomen, taking out a loop of intestine, emptying it so far as possible by gentle pressure, isolating its cavity by the application

of two ligatures 15 or 20 centimetres apart, and returning the whole into the abdominal cavity. After a few hours the animal was killed, and the fluid, which had collected in the isolated portion of intestine, taken out and examined. Colin adopted a similar method, but with greater precautions, in the horse. In one of these animals, while diges-

Fig. 51.



Loop of Small Intestine, from the horse, isolated by compressors, for obtaining intestinal juice. (Colin.)

tion was in full activity, he took out, through an opening in the left flank, a loop of small intestine, which he isolated by two compressors, made of flat wooden or metallic strips, enveloped by a ribbon of velvet, and fastened by screws in such a way that the inner surfaces of the intestine might be retained in close contact, without bruising or lacerating their tissues. The compressors being applied at a distance of from one to two metres apart after the included portion of intestine had been emptied by gentle pressure, the whole was returned into the abdomen, the external wound closed by sutures and the animal killed at the end of half an hour.

On the average, 100 grammes of fluid had accumulated within this time. It was clear, with a slightly yellowish or amber tint, alkaline in reaction, and with a specific gravity of 1010. According to the analysis of Lassaigne, it was composed as follows:

Composition of Intestinal Juice from the Horse.

Water	981.0
Albuminous matter	4.5
Sodium chloride, Potassium chloride, Sodium phosphate, Sodium carbonate	14.5
	1000.0

Thiry separated a portion of the small intestine from the remainder by two transverse sections, leaving the mesentery and vessels of the isolated portion uninjured, and then united by sutures the divided ends of the remaining portions, so as to re-establish the continuity of the intestine, but with a portion of it, 10 or 15 centimetres long, left out. Of this isolated portion, still nourished by its vessels, he closed one end by sutures, so as to make of it a blind extremity, while the other he fastened to the edges of the external wound in such a way as to make of it a permanent fistula. When all the parts had healed, and natural digestion was re-established, he collected the fluid discharged from the open end of the isolated portion of intestine. This operation has been repeated by other observers. The objection to it is that the isolated portion of intestine, after being for some weeks precluded from taking part in the process of digestion, becomes partially atrophied, and cannot be relied on as furnishing a secretion similar to the normal intestinal juice. The results obtained vary, some of them indicating that the secretion converts starch into sugar and has a dissolving action on coagulated albuminous matters, others that these properties are sometimes absent or but slightly developed.

On the whole, the method adopted by Frerichs and Colin, with its various modifications, seems to be the best and has furnished the most uniform results. Colin found that the fluid obtained in this way has the power of slowly transforming hydrated starch into sugar, and of emulsioning fatty matters with considerable energy. One part of olive oil, treated with five or six parts of intestinal juice, was transformed into a homogeneous mixture of a white color; and oil injected into the isolated portion of intestine, in the living animal, was found, after an hour, reduced to the condition of whitish homogeneous flakes.

Bernard obtained from a healthy dog which had been without food for twelve days, by an opening in the intestine 60 centimetres below the pylorus, a transparent, amber colored, alkaline fluid, which coagulated by heat, emulsioned oily matters distinctly though not strongly, and effected the transformation of hydrated starch. A small quantity of melted lard having been injected into the lower part of the intestine and a ligature placed above, at the end of an hour and a half the lower part of the intestine was found turgid, with emulsioned fat in its cavity, and its chyliferous vessels filled with opaque chyle.

It appears accordingly that the intestinal juice, so far as ascertained

by direct observation, is a comparatively scanty, alkaline fluid, containing an albuminous ingredient capable of coagulation by heat. It exerts an action upon starchy and fatty matters similar to that of the pancreatic juice, but less energetic in operation. Its action upon albuminous matters is less distinct, and has sometimes been found to be absent or feebly developed. It is undoubtedly of importance as accessory to the other digestive secretions, but the precise mode and extent of its operation have not yet been determined.

In the process of intestinal digestion a number of different actions are going on at the same time. The materials of the food, disintegrated and partly dissolved in the stomach, pass through the pylorus into the intestine still mingled with a notable quantity of gastric juice, and are there subjected to the action of the remaining digestive secretions. Hydrated starch, set free by the solution of the albuminous matters with which it was associated, rapidly undergoes the conversion into glucose, and the saccharine fluid so produced is promptly absorbed. If a dog be fed with a mixture of meat and boiled starch, although this conversion does not begin until the fluids enter the duodenum, we have found, in some instances, that at the end of three-quarters of an hour all traces of both starch and sugar had disappeared from both stomach and intestine. Raw starch in the lower animals is digested more slowly but in a similar manner. Bouchardat and Sandras, in examining the alimentary canal of the rabbit when fed with potato, found the grains of starch only slightly changed in the stomach, but in the small intestine they were altered, corroded, and more or less dissolved in proportion as they had descended the intestinal canal, while in the rectum only feeble traces of them remained.

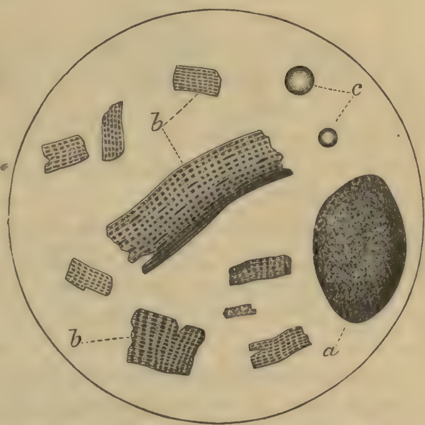
All observers agree that cane sugar undergoes the transformation into glucose by contact with the intestinal juices. This conversion may be slowly effected by the action of gastric juice alone. If one part of cane sugar be dissolved in 20 parts of dog's gastric juice, and kept at 38° (100° F.) the mixture will give traces of glucose at the end of two hours, and in three hours its quantity is considerable. It cannot be shown, however, that the gastric juice exerts this effect on sugar during ordinary digestion. If pure cane sugar be given to a dog with a gastric fistula while digestion of meat is going on, it disappears in from two to three hours, without any glucose being detected in the fluids withdrawn from the stomach. It is, therefore, either directly absorbed under the form of cane sugar, or passes, little by little, into the duodenum, where the intestinal fluids convert it into glucose.

Fatty matters, which are simply melted in the stomach, or set free by the liquefaction of the tissues which contain them, on entering the intestine begin to be emulsified by the pancreatic and intestinal juices. This process continues throughout the small intestine, together with the complete solution of muscular flesh which has been disintegrated by stomach digestion. If a dog, with a permanent duodenal fistula, be examined during the digestion of animal food, the fluid drawn from the fistula

within the first hour contains gastric juice, and is turbid with the remnants of disintegrated muscular tissue, mixed with fat vesicles and oil drops. This turbid mixture grows constantly thicker and more gruelly in consistency from the second to the tenth or the twelfth hour; after which the discharge of fluid from this part of the intestine becomes less abundant, and finally ceases almost completely, as digestion comes to an end.

The gradual alteration in the ingredients of the food may also be seen by killing the animal while digestion is going on, and examining the contents of the alimentary canal. If the food consisted of muscular flesh and adipose tissue, the stomach contains (Fig. 52) masses of softened meat, smeared over with gastric juice, and also a moderate quantity of a grayish grumous fluid with an acid reaction. This fluid contains muscular fibres, isolated from each other and more or less reduced to imperfect fragments. The fat vesicles of the solid adipose tissue of beef are but little altered, and there are only a few free oil globules to be seen floating in the mixed fluids in the cavity of the stomach. In the duodenum the muscular fibres are further disintegrated (Fig. 53). They become much broken up, pale, and transparent, but can still be recognized, under the microscope, by their characteristic granular markings and striations. The fat vesicles also begin to become altered in the duodenum. The solid granular fat of beef and similar kinds of meat becomes liquefied and emulsioned; and appears under the form of free oil drops and fatty molecules; while the fat vesicle itself is partially emptied, and becomes more or less collapsed and shrivelled. In the middle and lower parts of the intestine (Figs. 54 and 55) these changes continue. The muscular fibres become constantly more and more disintegrated, and a large quantity of granular debris is produced, which is at last also dissolved. The fat also progressively disappears, and the vesicles may be seen in the lower part of the intestine, collapsed and empty.

Fig. 52.

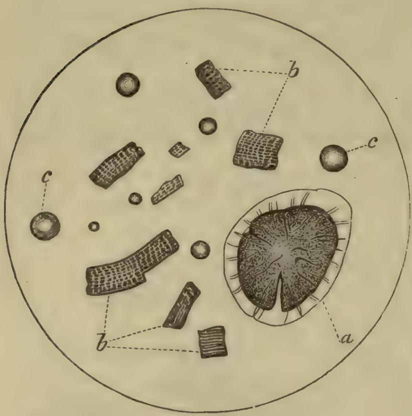


Contents of Stomach during Digestion of Meat, from the Dog.—*a.* Fat Vesicle, filled with opaque, solid, granular fat. *b, b.* Bits of partially disintegrated muscular fibre. *c.* Oil globules.

In this way the digestion of the different ingredients of the food goes on in a continuous manner, from the stomach throughout the entire length of the small intestine. At the same time, it results in the production of three different substances, namely: 1st. Albuminose, produced

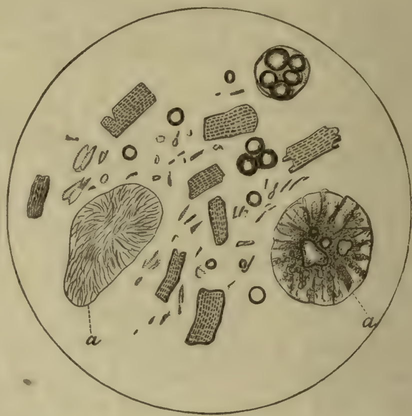
by the digestion of albuminous matters; 2d. A chylous fluid, from the emulsion of the fats; and 3d. Glucose, produced by the transformation

Fig. 53.



FROM DUODENUM OF DOG, DURING DIGESTION OF MEAT.—*a*. Fat vesicle, with its contents diminishing. The vesicle is beginning to shrivel and the fat breaking up. *b*, *b*. Disintegrated muscular fibre. *c*, *c*. Oil globules.

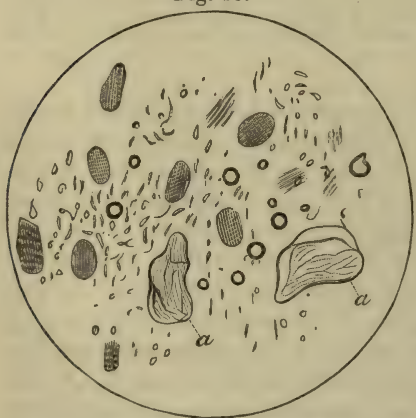
Fig. 54.



FROM MIDDLE OF SMALL INTESTINE.—*a*, *a*. Fat vesicles, nearly emptied of their contents.

of starch. These substances are then ready to be taken up into the circulation: and as the mingled ingredients of the intestinal contents pass successively downward through the intestine, the products of digestion, together with the digestive secretions themselves, are gradually absorbed by the vessels of the mucous membrane, and carried away by the current of the circulation.

Fig. 55.



FROM LAST QUARTER OF SMALL INTESTINE.—*a*, *a*. Fat vesicles, quite empty and shrivelled.

The Large Intestine and its Contents.

The mucous membrane of the large intestine is abundantly provided with tubular glandules which are not essentially different, in their anatomical characters, from the follicles of Lieberkühn. Their secretion, however, appears to be comparatively scanty, at least in the watery and albuminous ingredients which are present in the other intestinal juices. According to Ranke, fistulous openings in the large intestine do not yield any notable quantity of

fluid; and if a loop of the gut itself be isolated by ligatures, an accumulation of mucus-like matter is the only result. In the rabbit, however, after ligature of the vermiform appendix, Funke obtained, at the end of from two to four hours, a quantity of a turbid alkaline secretion, with which the appendix had become filled. This fluid was without action upon coagulated albumen; but it transformed starch into sugar, and also decomposed the sugar, with production of lactic and butyric acids. The same change was produced upon starch introduced into the cavity of the appendix.[1] This accounts for the acid reaction sometimes found in the cæcum of herbivorous animals, from the decomposition of undigested starch, although the mucous surface of the large intestine is constantly alkaline.

As the remnants of the alimentary mass pass the situation of the ileo-cæcal valve and enter the large intestine, they begin to acquire a more pasty consistency and a peculiar repulsive odor. Both these changes become more marked in the middle and lower part of the gut, until all the superfluous fluids have disappeared, and the consistency and odor of the feces are fully developed. This odor is not a putrefactive one, but is characteristic of the contents of the large intestine. Its source may be either a peculiar transformation of some of the ingredients of the food, or an excretory action of the mucous membrane of the intestine. It is probably in great part the result of an excretion, since in different kinds of animals, whatever be the nature of their food, the feces have usually a distinct odor characteristic of the species.

The average daily quantity of the feces in the human subject is 150 grammes, of which about 75 per cent. is water, and 25 per cent. solid residue. They consist, first, of the undigested remnants of the food; and, secondly, of the excreted materials from the alimentary canal. The undigested substances derived from the food are mainly animal or vegetable tissues, which, from their constitution, are incapable of digestion. These are elastic fibres, or bits of elastic tissue, which nearly always pass the intestine unchanged; shreds of tendon or fascia, not sufficiently softened by cooking; horny epidermic tissues, both animal and vegetable; and the spiral tubes and ducts of vegetable substances. The excreted materials of internal origin are the mucus of the large intestine, and probably also the volatile substances which produce the fecal odor. The coloring matters of the bile are present in a more or less altered form.

The mineral salts contained in the feces amount to a little over one-tenth of the solid ingredients. They are, for the most part, the same with those common to the animal fluids in general, but are mingled in different proportions; only about 4 per cent. consisting of the soluble chlorides and sulphates, while fully 80 per cent. are composed of lime and magnesium phosphates. They are regarded as mainly derived from

[1] Ranke, Physiologie des Menschen. Leipzig, 1872, p. 297.

the unabsorbed mineral ingredients of the food, and partly from the saline matters of the intestinal secretions.

Beside the above, the feces contain two crystallizable matters of organic origin, which, though not present in large quantity, are of importance from their chemical characters and the mode of their production; namely, excretine and stercorine.

Excretine.—This was discovered and described by Dr. W. Marcet,[1] as an ingredient of human feces, though it does not occur in those of the lower animals, either carnivorous or herbivorous. It is a neutral or faintly alkaline crystallizable substance, insoluble in water, but soluble in ether and hot alcohol. It crystallizes in radiated groups of four-sided prismatic needles. It fuses at 96° (204° F.), and burns at a higher temperature. It is non-nitrogenous, and consists of carbon, hydrogen, oxygen, and sulphur, in the following proportions:—

$$C_{78}H_{156}O_2S.$$

It is thought to be present mostly in a free state, but partly in union with certain organic acids, as a saline compound.

Stercorine.—This substance was discovered by Prof. A. Flint, Jr., both in human feces and in those of the dog, and was obtained by him in proportions varying from 0.07 to 0.3 per cent. of the entire fecal mass. It is most abundant in the feces of the human subject, where its average quantity is estimated by its discoverer as about 0.65 gramme per day. It is insoluble in water, soluble in ether and in boiling alcohol, neutral in reaction, and, like excretine, crystallizes in the form of radiating needles. It differs from excretine, however, in having a much lower fusion point, becoming liquefied at 36° (96°.8 F.). It is regarded as produced by transformation in the intestine from the cholesterine of the bile.[2]

[1] Philosophical Transactions. London, 1857, p. 410.

[2] American Journal of the Medical Sciences. Philadelphia, October, 1862.

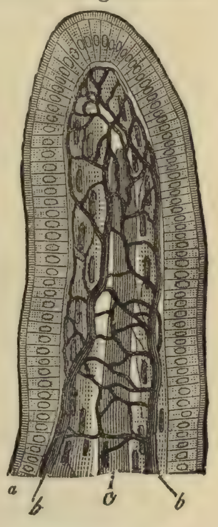
CHAPTER IX.

ABSORPTION.

THE mucous membrane of the small intestine, beside containing the glandular follicles already described, is provided with a special apparatus for the process of absorption. This apparatus consists of innumerable minute eminences or prolongations of its substance, so closely set over its free surface that they give to it a characteristic velvety appearance. These are the so-called villosities or *villi* of the small intestine. They are found throughout this part of the alimentary canal, from the pylorus to the free border of the ileo-cæcal valve, most abundant in the duodenum and jejunum, rather less so in the ileum, but in general in the proportion of from 20 to 40 to the square millimetre. In the upper part of the intestine they are flattened, laminated, or leaf-like in form, becoming cylindrical and filamentous in the middle and lower portions. In the human subject they are about one-half a millimetre in length.

Each villus consists of a mass of tissue continuous with that of the mucous membrane beneath. It is covered with a uniform layer of nucleated, finely granular cylindrical epithelium cells, closely united with each other by their lateral surfaces, and presenting at their outermost portion a thin layer which is more transparent than the rest of their substance, and is marked, according to Kölliker, Frey, and other observers, by fine vertical striations. The villus is penetrated from below by bloodvessels supplied from a terminal twig of the mesenteric artery, which form by their frequent division and inosculation an exceedingly abundant capillary network, almost immediately beneath the epithelial layer. At its base they reunite to form a venous branch, which is one of the commencing rootlets of the mesenteric vein.

Fig. 56.



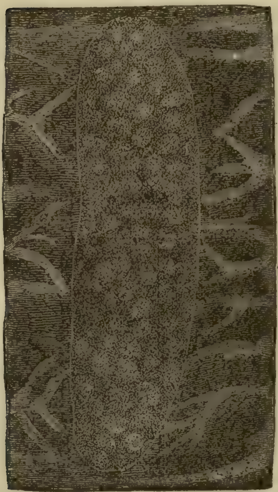
AN INTESTINAL VILLUS.—*a*. Layer of cylindrical epithelium, with its external transparent striated portion. *b b*. Bloodvessels entering and leaving the villus. *c*. Lymphatic vessel occupying its central axis. (Leydig.)

In the deeper part of the villus, and lying nearly in its longitudinal axis, there is also the commencement of a lymphatic vessel, which, after its emergence from the base of the organ, joins the general system of the abdominal lymphatic or lacteal vessels. The lymphatic vessel is usually single in the fili-

form or cylindrical villi, sometimes double or even triple in those of a more flattened form. It has exceedingly thin walls, consisting only of a single layer of flattened epithelium cells.

Closed Follicles of the Small Intestine.—In addition to the secreting glandules and villi, the intestine presents, throughout its extent, two sets of glandular looking organs, known as the *glandulæ solitariæ* and the *glandulæ agminatæ.* The first of these, or the solitary glandules, are found in the upper part of the intestine, scattered at intervals over its surface, as minute whitish points. Farther down they begin to occur in clusters of several together, and in the lower part of the jejunum and in the ileum they constitute rounded or elongated oval patches, from $1\frac{1}{2}$ to 5 centimetres in length, known by the name of "Peyer's patches." These patches are always situated opposite the attachment of the mesentery, and with their long diameter parallel to the axis of the intestine.

Fig. 57.

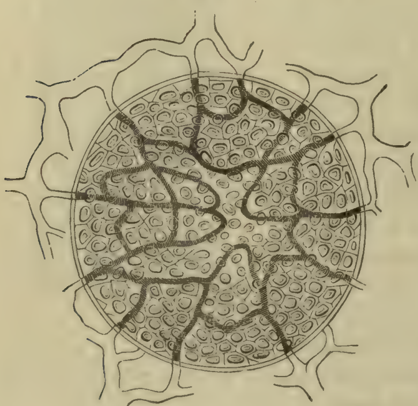


Peyer's Patch of agminated glandules from the ileum. (Boehm.)

The structure of the solitary glandules and of those forming Peyer's patches is the same. The only difference between them is that in one case the follicles are distributed separately over the surface of the intestine, while in the other they are collected into distinct groups.

Each follicle is a rounded or ovoid body, from one-half to two millimetres in diameter, situated partly in the thickness of the mucous membrane, and partly below. It consists of an external investing capsule, closed on all sides, from the inner surface of which slender anastomosing filaments pass through the substance of the organ, forming a delicate scaffolding or framework of minute fibres. In the interstices between these fibres there is a small quantity of fluid, together with an abundance of *lymph corpuscles*, or faintly granular cells about 13 mmm. in diameter. The follicle is also

Fig. 58.



One of the closed Follicles of Peyer's Patches, from Small Intestine of Pig, showing the bloodvessels in its interior. Magnified 50 diameters.

penetrated by capillary bloodvessels, which pass through its investing capsule from without, inosculate freely with each other in its interior, and return upon themselves in loops near its centre.

The follicles have a close relation with the lymphatics of the intestine. The lymphatic vessels coming from the villosities form a plexus in the substance of the mucous membrane from which branches pass to the follicles and ramify upon their surface, forming another close plexus upon their investing capsule. The lymphatic vessels, however, do not penetrate into the interior of the follicles, which are occupied by bloodvessels alone Owing to the analogy in structure between these bodies and portions of the lymphatic glands, as well as to the fact that the lacteals coming from the neighborhood of Peyer's patches are more numerous than from other points of the intestine, the closed follicles are generally regarded as belonging to the system of the lymphatic glands. They constitute the simplest form of these glands, situated in or immediately beneath the intestinal mucous membrane. They furnish no fluid secretion to the intestinal cavity, but are connected in some way with the preparation or elaboration of the absorbed materials.

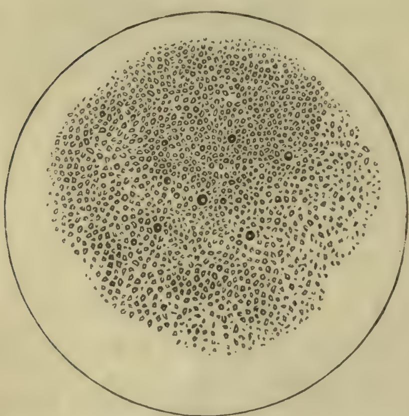
Mechanism of Absorption by the Villi.—The villi are the active agents in the process of absorption. The entire extent of the mucous membrane of the small intestine, including the valvulæ conniventes, is estimated at about 6000 square centimetres of surface; and as the number of the villi is, on the average, not less than 30 to the square millimetre, there must be at least from fifteen to twenty millions of them in the whole length of the small intestine. By their great abundance, accordingly, as well as by their projecting form, they multiply the extent of surface over which the digested fluids come in contact with the intestinal mucous membrane, and increase, to a corresponding degree, the energy with which absorption takes place. They hang out into the nutritious, semi-fluid mass contained in the intestinal cavity, as the roots of a tree penetrate the soil; and they imbibe the liquefied portions of the food with a rapidity which is in direct proportion to their extent of surface and the activity of the circulation.

The process of absorption is also hastened by the peristaltic movements of the intestine. The muscular layer here, as in other parts of the alimentary canal, is double, consisting of both circular and longitudinal fibres. The action of these fibres may be readily seen by pinching the exposed intestine with the blades of a forceps. A contraction takes place at the spot irritated, by which the intestine is reduced in diameter, its cavity partially obliterated, and its contents forced onward into the succeeding portion of the alimentary canal. The local contraction then propagates itself to the neighboring parts, while the portion originally contracted becomes relaxed; so that a slow, continuous, creeping motion of the intestine is produced, by successive waves of contraction and relaxation, which follow each other from above downward. At the same time, the longitudinal fibres have a similar alter-

nating action, drawing the narrowed portions of intestine up and down, as they successively enter into contraction or become relaxed in the intervals. The effect of the whole is to produce a peculiar, writhing, worm-like, or "vermicular" motion, among the different coils of intestine. During life, the vermicular or peristaltic motion of the intestine is excited by the presence of food undergoing digestion. By its action, the substances which pass from the stomach into the duodenum are steadily carried from above downward, so as to traverse the entire length of the small intestine, and to come in contact successively with the whole extent of its mucous membrane. During this passage the absorption of the digested food is constantly going on. Its liquefied portions are taken up by the villi of the mucous membrane, and successively disappear; so that, at the termination of the small intestine, there remains only the undigested portion of the food, together with the refuse of the intestinal secretions. These pass through the ileo-cæcal orifice into the large intestine, and there become reduced to the condition of feces.

The digested fluids taken up from the intestine are first absorbed by the epithelial cells covering the surface of the villi, and are thence transmitted to the deeper portions of their tissue. This passage of the products of digestion through the substance of the epithelial cells is difficult of demonstration for perfectly homogeneous liquids, but it may be distinctly seen in the case of the fatty matters of the chyle. As already described, the oleaginous matters of the food are emulsified by digestion, forming in the intestine a white milky fluid, termed the "chyle," which is entangled in the folds of the mucous membrane, and adheres to the surface of the villi. In chyle which is drawn either from the lacteal vessels or the thoracic duct, the fatty matter still presents itself in the same condition, and retains all the chemical properties of oil. Examined by the microscope, it is seen to exist under the form of fine granules and molecules, varying in size from 2.5 mmm. downward, which present the ordinary appearances of oil in a state of minute subdivision. The chyle, therefore, does not represent the entire product of the digestive process, but consists of the fatty substances, suspended by emulsion in a serous fluid.

Fig. 59.



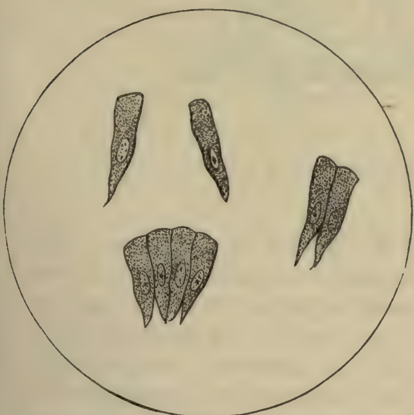
Chyle from commencement of Thoracic Duct, from the Dog.

The emulsioned oil has accordingly passed from the cavity of the

intestine into that of the lacteal vessels. Its transmission is facilitated by the alkaline condition of the blood and of the intestinal juices. Oil by itself is a non-diffusible substance; that is, it is incapable of passing through an animal membrane by endosmosis. If a fluid containing oil be placed on one side of an animal membrane, and pure water on the other, the water will readily penetrate the substance of the membrane, while the oily particles cannot be made to pass under any ordinary pressure. Though this be true, however, for pure water, it is not true for slightly alkaline fluids like the serum of blood or the lymph. This has been demonstrated by the experiments of Matteucci, in which he made an emulsion with an alkaline fluid containing 4.3 parts per thousand of potassium hydrate. Such a solution has no perceptible alkaline taste, and its action on reddened litmus paper is about equal to that of the lymph and chyle. If this emulsion were placed in an endosmometer, together with a watery alkaline solution of similar strength, it was found that the oily particles penetrated the animal membrane without much difficulty, and mingled with the fluid on the opposite side. Endosmosis will thus take place with a fatty emulsion, provided the fluids used in the experiment be slightly alkaline in reaction.

The fatty molecules of the chyle, accordingly, are taken up by the layer of epithelium cells covering the surface of the villi, and their passage into and through the epithelial layer produces a marked alteration in the physical appearance of the cells composing it. In the intervals of digestion these cells are nearly transparent and homogeneous-

Fig. 60.



INTESTINAL EPITHELIUM; from the Dog, while fasting.

Fig. 61.

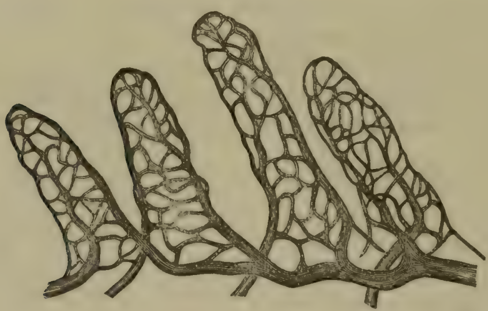
INTESTINAL EPITHELIUM; from the Dog, during the digestion of fat.

looking, presenting under the microscope only the appearance of a very fine and delicate granulation. (Fig. 60.) But if examined during the digestion and absorption of fatty matters, their substance is seen to be

crowded with oily particles, taken up by absorption from the intestinal cavity. (Fig. 61.) The oily matter then passes onward, penetrating deeper into the substance of the villus, until it is at last received by the capillary vessels in its interior.

Absorption by the Bloodvessels.—The final absorption of the digested fluids is accomplished mainly by the bloodvessels of the intestinal villi. Their situation, their numbers, and the rapid movement of the blood through these channels, are all circumstances especially favorable for the performance of this function. The capillary plexus of each villus is situated in the most superficial part of its substance, almost immediately beneath the epithelium cells which cover its surface, so that the absorbed fluids, after passing through the epithelial layer, come at once in contact with the capillaries of the vascular network. The extension of absorbing surface, from the repeated division and inosculation of these vessels, and the constant renovation of the fluids which they contain, by the movement of the circulation, provide for their constant activity, and drain away the absorbed fluids from the substance of the villus as fast as they are taken up by its exposed surface.

Fig. 62.



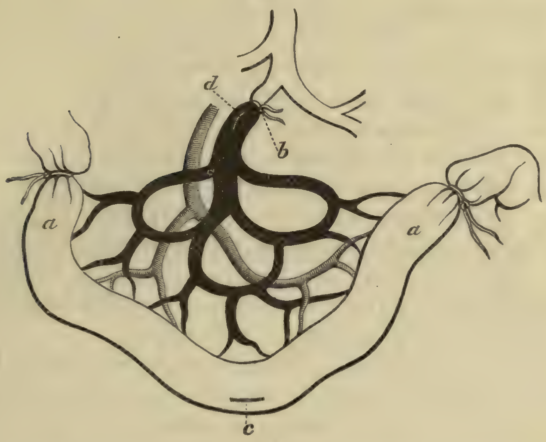
Capillary Bloodvessels of the Intestinal Villi; from the Mouse. (Kölliker.)

The activity of the bloodvessels in the process of absorption is also a matter of direct observation. Abundant experiments have demonstrated, not only that soluble substances introduced into the intestine may be soon afterward detected in the blood of the portal vein, but that absorption takes place more rapidly and abundantly by the bloodvessels than by the lacteals. This was first shown by Magendie,[1] who found that the absorption of poisonous substances would take place, in the living animal, both from the cavity of the intestine and from the tissues of the lower extremity, notwithstanding that all communication through the lacteals and lymphatics was cut off, and the passage by the

[1] Journal de Physiologie. Paris, 1825, tome i. p. 18.

bloodvessels alone remained. These results were afterward corroborated by Panizza, who succeeded in detecting the substance which had been absorbed in the venous blood returning from the part. This observer opened the abdomen of a horse, and drew out a fold of the small intestine, about 20 centimetres in length (Fig. 63, *a*, *a*), which he included

Fig. 63.



PANIZZA'S EXPERIMENT.—*aa*. Intestine. *b*. Point of ligature of mesenteric vein. *c*. Opening in intestine for introduction of poison. *d*. Opening in mesenteric vein behind the ligature.

between two ligatures. A ligature was then placed (at *b*) upon the mesenteric vein receiving the blood from this portion of intestine; and, in order that the circulation might not be interrupted, an opening was made (at *d*) in the vein behind the ligature, so that the blood brought by the mesenteric artery, after circulating in the intestinal capillaries, passed out at the opening, and was collected in a vessel for examination. Hydrocyanic acid was then introduced into the intestine by an opening at *c*, and almost immediately afterward its presence was detected in the venous blood flowing from the orifice at *d*. The animal, however, was not poisoned, since the acid was prevented from gaining an entrance into the general circulation by the ligature at *b*.

Panizza afterward varied this experiment in the following manner: Instead of tying the mesenteric vein, he simply compressed it. Then, hydrocyanic acid being introduced into the intestine, as above, no effect was produced on the animal, so long as compression was maintained upon the vein. But as soon as the blood was again allowed to pass through the vessels, symptoms of general poisoning became manifest. Lastly, in a third experiment, the same observer removed all the nerves and lacteal vessels supplying the intestinal fold, leaving the bloodvessels alone untouched. Hydrocyanic acid, now being introduced into the intestine, found an entrance at once into the general circulation, and

the animal was immediately poisoned. The bloodvessels, therefore, are not only capable of absorbing fluids from the intestine, but take them up even more rapidly than the lacteals.

The entrance of digested materials into the bloodvessels of the intestine is readily demonstrated in a similar way. After the digestion of food containing a mixture of albuminous and starchy ingredients, both sugar and albuminose are to be met with in the blood of the mesenteric and portal veins. Digested and emulsioned fatty matters may also be distinctly followed, in their passage through the same channels, by the turbid and chylous aspect which they communicate to the portal blood. It is easy to see that the blood of the portal system, in the carnivorous animals during digestion, contains fatty matter in a state of minute subdivision, similar in appearance to that found in the chyle and in the substance of the villi, often so abundant as to communicate a turbid appearance to the serum after coagulation; and various observers (Lehmann, Schultz, Simon), in examining the blood from different parts of the body, have also found the blood of the portal system considerably richer in fat than that of the arteries or of other veins, particularly while intestinal digestion is going on with activity.

Absorption by the Lacteals.—The absorption of digested materials, but more particularly of the fatty matters, is also accomplished by the lymphatics or lacteals of the small intestine. These, however, do not form a distinct class of vessels by themselves, but are simply a part of the great system of lymphatic or absorbent vessels, which are to be found everywhere in the integuments of the head, the parietes of the trunk, the upper and lower extremities, and in the glandular and muscular organs and mucous membranes throughout the body. Originating in the tissues of the above mentioned parts, they pass from the periphery toward the centre, their branches converging and uniting with each other like those of the veins, and passing, at various points in their course, through certain glandular-looking bodies, known as the lymphatic glands.

The fluid generally contained in these vessels is called the "lymph." It is a colorless or slightly yellowish transparent liquid, which is absorbed by the lymphatic vessels from the tissues in which they originate. So far as regards its composition, it is known to contain, beside water and saline matters, a small quantity of fibrine and albumen. Its ingredients are evidently derived from the metamorphosis of the tissues, and are returned to the centre of the circulation to be eliminated by excretion, or to undergo some new transforming process, the details of which are not as yet fully understood.

The lymphatic vessels of the intestine originate, as we have seen, in the substance of the villi, where they commence by longitudinal spaces lined with flattened epithelium cells, becoming provided, at a short distance from their origin, with thin, transparent, elastic coats, like those of the capillary bloodvessels. After leaving the base of the villi they become part of the lymphatic plexus, from which the main branches pass

inward, between the layers of the mesentery, from the intestine toward the posterior part of the abdomen. During their course through the mesentery, they inosculate with each other by transverse branches, and pass in succession through several ranges of mesenteric glands, which have the same structure with those already mentioned, and which are accordingly the lymphatic glands of the abdominal cavity. On arriving near the attached portion of the mesentery, on the right side of the abdomen, at about the level of the second lumbar vertebra, they terminate in a saccular dilatation, known as the "receptaculum chyli." From this point the thoracic duct passes upward through the cavity of the chest, crossing obliquely from the right to the left of the median line, and finally discharges its contents into the left subclavian vein, at its junction with the jugular of the same side.

In the intervals of digestion the fluid contained in the lymphatic vessels is the same in appearance throughout the body. Its colorless and transparent character, together with the small size of the lymphatics themselves, and the thinness and delicacy of their coats, make these vessels nearly or quite invisible to the unaided eye. But during the digestion and absorption of food the elements of the chyle are taken up by the lymphatics of the small intestine, which are distended with a milky fluid, and thus become visible as an abundant network of opaque white filaments, ramifying in the intestinal walls, converging from the intestine to the receptaculum chyli, and contrasting strongly with the ruddy and semi-transparent color of the neighboring tissues. If, when in this condition, one of them be opened with the point of a scalpel, it discharges a chylous liquid, which is easily seen to be the same in character with that contained in the cavity of the intestine itself, namely, an emulsion of fatty molecules and granulations. Owing to the appearance thus given to the vessels themselves, and to the milky fluid which they contain, they have received the name of the *lacteals*, or lactiferous vessels of the abdomen.

The presence of chyle in the lacteals is, therefore, not a constant, but only a periodical phenomenon. The fatty substances constituting the chyle begin to be absorbed during the process of digestion, as soon as they have been disintegrated and emulsioned by the action of the intestinal fluids. As digestion proceeds, they accumulate in larger quantity, and gradually fill the whole lacteal system, giving to its vessels the characteristic aspect above described. But as digestion and absorption from the intestinal cavity come to an end, the milky fluid disappears from the lymphatics, and they resume their former transparent and colorless appearance.

The lacteals accordingly are nothing more than the lymphatics of the small intestine, which, in addition to the transparent and colorless lymph which they usually contain, have absorbed a fluid rich in fat derived from the process of digestion. While this process is going on, they are distinguished from the lymphatics elsewhere by the milky character of their contents, which accumulate in the receptaculum chyli,

and may be followed thence through the thoracic duct, to the point where it terminates in the left subclavian vein.

It was owing to the opacity and visibility of the lacteals during digestion that these vessels were discovered in 1622 by Asellius, who first saw them on opening the abdomen of a dog, a few hours after the ingestion of food. The discovery of the general system of lymphatic vessels was made subsequently by Rudbeck and Bartholin, in 1651 and 1653, and was consequent upon the previous observations on the lacteals of the abdomen.

Fig. 64.

Lacteals and Lymphatics, during digestion.

That the white color of the chyle during digestion is really due to the presence of fatty substances absorbed from the intestine. is shown by the fact that the intensity of this color is in proportion to the quantity of fat contained in the food. It is generally less marked in herbivorous than in carnivorous animals. According to the observations of Tiedemann and Gmelin, in a dog fed with fatty matters the lacteals are abundantly filled with an opaque white fluid, while in the same animal fed with starchy matters alone, the chyle is pale and but slightly opaline; and finally Bernard has shown that if, in a dog after several days fasting, a little ether, containing fat in solution, be injected into the stomach, without the introduction of any other food, at the end of a few hours the lacteals are found fully distended with milky chyle, precisely similar in appearance to that obtained during ordinary digestion.

Passage of Absorbed Materials into the Circulation.—The products of digestion, which are taken up by the bloodvessels and lymphatics of the intestine, pass by two different routes into the general circulation. The blood of the portal system, containing albuminose, sugar, and molecular fat, is carried at once to the liver, where it traverses the capillary vessels of this organ before reaching the vena cava and the

right side of the heart. The chyle, on the other hand, containing also a large proportion of fatty ingredients, passes by the thoracic duct directly to the left subclavian vein and is there mingled with the returning current of the venous blood. But all these substances, after entering the circulation and coming in contact with the organic ingredients of the blood, are modified in such a way as no longer to be recognizable under their original form. This change takes place very rapidly with the albuminose and the sugar, both of which are taken up in greatest proportion by the bloodvessels and are carried at once through the hepatic capillaries. The albuminose passes, in all probability, into the condition of ordinary albumen, while the sugar rapidly becomes decomposed, or transformed, and loses its characteristic properties; so that, on arriving at the entrance of the general circulation, both these newly absorbed ingredients have become already assimilated to those which previously existed in the blood. The fatty matters also, which reach the blood on the right side of the heart both by the portal and hepatic veins, and by the thoracic duct and subclavian vein, undergo a transformation while passing through the lungs by which their distinctive characters are destroyed, and they are no longer visible as oleaginous molecules. This alteration is so complete, during the early part of digestion, or when the proportion of fat in the food is small, that all the oleaginous matter disappears in the lungs and none of it is to be detected in the blood of the general circulation.

But as digestion proceeds, especially when the food has been abundant in oleaginous substances, an increasing quantity of fatty matter finds its way, by these two passages, into the blood; and a time at last arrives when the whole of the fat so introduced is not destroyed during its passage through the lungs. Its absorption taking place at this time more rapidly than its decomposition, it begins to appear, in moderate quantity, in the blood of the general circulation; and, lastly, when the intestinal absorption is at its point of greatest activity, it is found in considerable abundance throughout the entire vascular system. At this period, some hours after the ingestion of food rich in oleaginous matters, the blood, not only of the portal vein, but also of the general circulation, everywhere contains a superabundance of fat, derived from the digestive process. If blood be then drawn from the veins or the arteries in any part of the body, it will present the peculiar appearance known as that of "chylous" or "milky" blood. On the separation of the clot the serum is turbid; and after a few hours of repose, the fatty substances which it contains rise to the top and cover its surface with a partially opaque and creamy-looking pellicle. This appearance has been occasionally observed in the blood of the human subject, particularly in cases of apoplexy occurring after a full meal. It is a purely normal phenomenon, and depends simply on the rapid absorption, at certain periods during the digestive process, of oleaginous substances from the intestine. It can be observed in the dog at any time by feeding him with

fat meat, and drawing blood, seven or eight hours afterward, from the carotid artery or the jugular vein.

This state of things continues for a varying length of time, according to the amount of oleaginous matters contained in the food. When digestion is terminated, and the fat ceases to be introduced in unusual quantity into the circulation, its transformation and decomposition continuing to take place in the blood, it disappears gradually from the veins, arteries, and capillaries of the general system; and, finally, when the whole of it has been disposed of by the nutritive process, the serum again becomes transparent, and the blood returns to its ordinary condition.

In this manner the nutritive elements of the food, prepared for absorption by the digestive process, are taken up into the circulation under the different forms of albuminose, sugar, and chyle, and accumulate as such, at certain times, in the blood. But these conditions are temporary and transitional. The nutritive materials soon pass by transformation into other forms, and become assimilated to the pre-existing elements of the circulating fluid. In this way they accomplish finally the object of digestion, and replenish the blood by a supply of new materials from without.

CHAPTER X.

THE BILE.

The first peculiarity of the liver, as compared with other secreting organs, is that it is supplied with blood at the same time from two different sources; namely, from the hepatic artery and the portal vein. The ramifications of the hepatic artery are especially distributed to the walls of the hepatic ducts, to those of the portal vein, to the capsule of Glisson, and to the peritoneal covering of the organ; while those of the portal vein pass in a peculiar manner into the glandular parenchyma, and after traversing its substance as a capillary plexus become continuous with the rootlets of the hepatic vein. Beside arterial blood, accordingly, which it receives in common with the other abdominal organs, in moderate quantity, it is supplied with an abundance of venous blood, collected by the portal system from the stomach, the spleen, the pancreas and the intestinal canal.

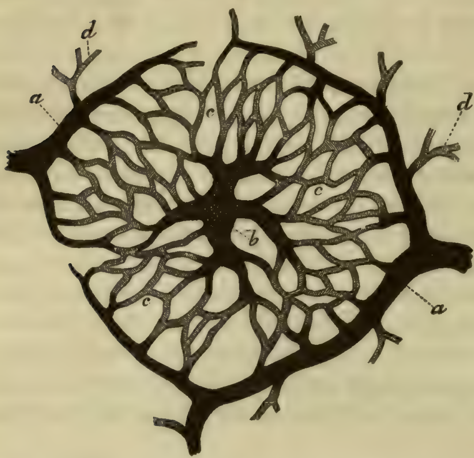
Secondly, the liver is distinguished by its large size. While the weight of all the salivary glands taken together, in the human species, is but little over 100 grammes, and that of the pancreas about 75 grammes, the liver forms a compact vascular and glandular organ, weighing nearly or quite 1600 grammes, and occupying a considerable portion of the abdominal cavity.

Lastly, the liver is peculiar in its texture, and differs so much in this respect from the other secretory organs, as to require a special description. As in other instances, the secreting apparatus consists essentially of glandular cells and capillary bloodvessels, with the ducts which collect and transport the secreted fluid; but these elements, instead of being arranged as elsewhere in distinct groups of tubular or rounded follicles, are closely united with each other, forming on all sides a continuous mass by their mutual contact and adhesion.

The substance of the liver, in man and in the quadrupeds generally, is divided into pentagonal or hexagonal masses or islets, about 1.5 millimetre in diameter, which are known by the name of the hepatic *lobules*. These lobules, however, are not distinctly separated from each other, but are simply made visible by the relative arrangement of the afferent and efferent bloodvessels. Each lobule is embraced upon its external surface by the terminal branches of the portal vein, which ramify between the lobules lying adjacent to each other. These vessels are accordingly known as the *interlobular veins*. From the side of the interlobular vein, minute vessels pass into the substance of the lobule, and there form by their division and inosculation an abundant capillary

plexus, the vessels of which have a general convergent direction from the periphery toward the centre. At the middle part of the lobule they unite to form the commencement of an efferent vessel which, from its central or interior position, is termed the *intralobular* vein. This rootlet continues its course until it joins one of the smaller branches of the hepatic vein. Each lobule may therefore be considered as a more or less ovoid, cylindrical or prismatic mass, resting upon a branch of the hepatic vein, and attached to this vessel by its own intralobular vein, which passes through its axis and receives the blood collected from its capillary vessels; while it is encircled by terminal branches of the portal vein supplying the blood for its interior circulation.

Fig. 65.



HEPATIC LOBULE, in transverse section, showing the distribution of its bloodvessels.—*a*, *a*. Interlobular veins. *b*. Intralobular vein. *c*, *c*, *c*. Plexus of Capillary bloodvessels in the substance of the lobule. *d*, *d*. Twigs of interlobular vein, passing to adjacent lobules.

Beside its capillary bloodvessels, the mass of the lobule is made up mostly of glandular cells. These cells are generally of a five- or six-sided prismatic form, often with one or two of their borders excavated by curvilinear furrows at the points where they are in contact with a capillary bloodvessel. They are, on the average, 22 mmm. in diameter, of a finely granular aspect, usually, in the human subject, containing one or more minute fat globules, and provided with a well-marked round or oval nucleolated nucleus. The cells are everywhere in contact with each other by their plane surfaces, and each one is also in direct relation at several points with a capillary bloodvessel. Thus

Fig. 66.

GLANDULAR HEPATIC CELLS. From the human liver.

the union of these two elements is intimate and complete throughout the substance of the hepatic lobule.

There is an equally close connection between the glandular substance of the liver and the biliary ducts. The main hepatic duct, which with its ramifications accompanies the divisions of the portal vein, breaks up into branches which finally reach the interlobular spaces. The biliary ducts in the human liver which have a larger diameter than about 200 mmm. are lined with cells of cylindrical epithelium; while in those which are below 100 mmm. in diameter, the form of the cells changes gradually to that of pavement epithelium. The biliary ducts which occupy the interlobular spaces are of the smaller variety, being not more than 50 mmm. in diameter, and are lined accordingly with pavement epithelium. They break up into communicating branches which cover the surface of the lobule with a plexus of biliary canaliculi.

Fig. 67.

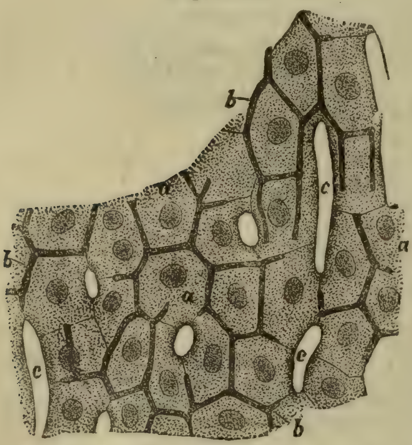
FINER BILIARY CANALS AND BILIARY DUCTS, from the frog's liver.—*a*. Small biliary duct, with its lining of epithelium cells. *b*, *c*. Terminal branches of the minute biliary canals, surrounded by glandular cells. *d*. Transverse communicating branch between two biliary canals. *e*, *e*. Sheath of glandular secreting cells, surrounding the biliary canals. *f*. Section of capillary bloodvessel. (Eberth.)

From this superficial plexus the finest biliary tubes penetrate into the substance of the lobule and there inosculate with each other between the glandular secreting cells. In the liver of the amphibia (frogs and water-lizards), as shown by the investigations of Hering and Eberth, the ultimate structure of the secreting apparatus is not essentially different from that of other lobulated glands. The smaller biliary ducts, lined with pavement epithelium, give off minute branches which communicate with each other more or less abundantly and are themselves in contact everywhere with the large glandular cells; each terminal branch being

surrounded by a single sheath of such glandular cells, which stand in place of the epithelial lining of a tube or follicle.

In the liver of the warm-blooded quadrupeds, the texture of the organ is more compact, the glandular cells and capillary bloodvessels more closely united, and especially the finest biliary passages in the substance of the lobule are more abundant and inosculate more frequently with each other. From the plexus of biliary canaliculi upon the surface of the lobule, already described, branches of much smaller size penetrate into its interior, and these inosculate so abundantly by transverse communications that they encircle each glandular cell in the meshes formed by their network. These interior communicating passages are the *capillary bile-ducts.* They are much smaller than the capillary bloodvessels, being in the rabbit's liver, according to Kölliker, not more than 2 mmm. in diameter, regularly cylindrical in form, and without any perceptible dilatations at the points of inosculation. They embrace the glandular cells in such a way that they are always situated at the greatest possible distance, that is, half the diameter of a cell, from the nearest capillary bloodvessel; the bloodvessels running along the borders or angular edges of the prismatic cells (Kölliker), while the capillary bile-ducts pass along the middle of their plane surfaces. Thus, the two sets of canals, namely, capillary bloodvessels and bile-ducts, form a double series of inosculating passages embracing the glandular cells, the meshes of which are always directed nearly or quite at right angles to each other.

Fig. 68.



Transverse Section of Part of a Lobule from the Rabbit's Liver.—*a, a, a.* Nucleated glandular cells. *b, b, b.* Capillary bile-ducts passing between the adjacent cells. *c, c, c.* Sections of capillary bloodvessels. (Genth.)

The intralobular capillary bile ducts, above described, as demonstrated by injections, have been regarded by some authorities as artificially produced by the accidental extravasation of the injection fluid and its infiltration between the glandular cells. But the existence of these ducts as a natural formation has been corroborated by too many observers to leave it a matter of doubt, especially considering the regular and uniform arrangement under which they present themselves. Their situation is also against the hypothesis of their artificial origin, since they are not placed at the angular borders of the glandular cells, where an extravasated fluid would naturally find its way, but run along the middle of their plane surfaces where they lie in close contact with each other; and,

finally, Kölliker has found that the capillary bile ducts in the liver of the rabbit may become visible in their usual positions in thin sections hardened in alcohol, where no injection has been practised. They are, therefore, to be regarded as the finest commencing ramifications of the biliary canals, which receive the secreted fluids directly from the substance of the glandular cells.

Physical and Chemical Characters of the Bile.—The bile is distinguished from all the other secretions discharged into the alimentary canal principally by the fact that it does not contain any albuminous ingredient analogous to those of the saliva, the gastric, pancreatic, or intestinal juices; its most important constituents being nitrogenous crystallizable substances, together with cholesterine and coloring matters. Bile taken from the gall-bladder contains, it is true, a certain amount of mucus, which gives it more or less of a ropy and viscid character; but this mucus is secreted by the gall-bladder itself, and bile taken from the gall-ducts in the substance of the organ is always perfectly fluid and watery in consistency. Furthermore, the gall-bladder is by no means constantly present, even in the higher animals, being absent, according to Wagner, in the horse, the camel, most of the pachydermata and several of the gnawing animals, and at the same time present in many closely allied species. The bile accordingly, in its essential ingredients, differs in a marked degree from the digestive secretions proper.

The bile, as it comes from the gall-bladder, is a clear, more or less tenacious and ropy fluid, neutral in reaction, with a faint and rather indefinite animal odor. If it be shaken up with air, or if air be blown into it through a narrow tube, it easily foams up into a frothy mixture which remains for a long time on the surface of the fluid. This property of frothing upon agitation with air does not depend upon the mucus which it contains, but upon the biliary salts proper, namely, the sodium glycocholate and taurocholate; since these salts in a pure watery solution exhibit the same property.

Its specific gravity is rather high, as compared with that of the other secretions. In ox-bile, we have found it to be 1024, in pig's bile 1030 to 1036. The specific gravity of human bile, according to Robin, is from 1020 to 1026; according to Jacobsen, in bile from a biliary fistula, but little over 1010. We have found it, in bile taken from the gall-bladder, 1018.

Its color varies, in different species of animals, from a reddish-orange to a nearly pure green, and in different instances presents all the intermediate tints of golden-yellow, reddish-brown, olive-brown, olive, yellowish-green, and bronze-green. It may be described in general terms as a greenish-bronze, with sometimes more or less of an orange tint. Human bile from a biliary fistula was found by Jacobsen to be of a clear yellowish bronze-green; that taken from the gall-bladder after death is usually of a dark golden-brown. Dog's bile is of a brownish-olive or bronze color; pig's bile of a reddish-orange or reddish-brown;

and sheep and ox-bile of a greenish-olive, or more frequently of a pure green. As a general rule, the bile of the herbivorous animals is more decidedly green in hue, that of the carnivora and omnivora orange or brown. All these differences may be referred to two main classes of tints, corresponding with two different coloring matters; in one of which the predominating color is red or reddish-brown, dependent on *bilirubine*, while in the other it is green owing to the presence of *biliverdine*. As the proportion of these two substances varies in any given specimen, it will exhibit a corresponding color of the pure or mingled tints.

The color of the bile is also modified by oxidizing agents, which produce a green hue in bile which was originally olive or brown, and increase the intensity of the green tint when this color is already present. If brown or olive-colored bile be exposed to the air for a short time, its surface becomes green by contact with the atmosphere. The same change may be instantly produced by adding to the bile a few drops of a watery solution of iodine; and a little nitric acid acts with great energy, developing a bright grass-green hue. These changes depend upon the oxidation of the bilirubine, and its consequent conversion into biliverdine.

The green color of bile also disappears rapidly when excluded from all sources of oxidation. If ox-bile, of a pure green or olive-green hue, be inclosed in a perfectly full and securely stoppered vessel, so as to be entirely protected from the air, it gradually loses its green color and becomes of a dull yellow. This change progresses from the external parts of the liquid toward its centre, until at the end of twelve, twenty-four, or thirty-six hours the whole of it has become of a light yellow or yellowish-brown. In this condition the green hue may be again restored by the addition of iodine, or by exposing the bile in thin layers to the air. The green color of the bile accordingly appears to be dependent on continued oxidation.

The bile presents, in addition, certain remarkable optical properties which distinguish it from other animal fluids.

In the first place, it is *dichroic;* that is, it has two different colors by transmitted light, according to the thickness of its mass. If ox-bile, which is of a pure transparent green by ordinary daylight in layers of two or three centimetres, be viewed by strong sunlight in a thickness of five or six centimetres, it is red. In this respect it resembles a solution of chlorophylle, which presents the contrast of the same two colors in a very marked manner.

Secondly, the bile is *fluorescent;*[1] that is, it becomes faintly luminous

[1] This property, so called from *fluor spar*, in which it was first observed, is shown by various transparent substances, when illuminated by solar light, or by that of certain parts of the spectrum. Thus a solution of quinine sulphate, which is perfectly colorless by ordinary diffused daylight, becomes blue at any spot where the sun's rays are concentrated upon it by a lens; and it exhibits a distinct luminosity in both the violet and ultra-violet parts of the spectrum.

with a color of its own, when viewed by the more refrangible rays of the solar spectrum. If a specimen of bile, of a clear greenish color, be placed in the track of either the violet or blue rays of the solar spectrum, it becomes visible with a light yellowish-green tint. In the green it is more yellowish; and in the yellow it has a distinct tinge of red; while in the red ray its fluorescence is hardly perceptible. Thus in all parts of the spectrum where it exhibits this property, it emits a light of less refrangibility than that of the ray by which it is illuminated. The property of fluorescence is also manifested, to a remarkable degree, by solutions of chlorophylle, which, although of a clear green color by diffused daylight, are of a pure red, when viewed by either the violet, blue, green, or yellow rays of the spectrum.

The fluorescence of bile, however, does not depend altogether upon its coloring matter, but is due mainly to the presence of the biliary salts, since it is exhibited in an equal degree by watery or alcoholic solutions of sodium taurocholate and glycocholate; the only difference being that the color of these solutions by the violet and blue rays is nearly pure yellow instead of yellowish-green.

Thirdly, the *spectrum* of bile is distinguished by certain peculiar characters and absorption bands, dependent upon its coloring matter.[1] All the more refrangible rays are absorbed with great intensity, so that the visible spectrum is very short, terminating usually within the limits of the green, about midway between the lines E and F. A portion of the green, accordingly, and the whole of the blue, indigo, and violet are completely absorbed, even when the bile is viewed in a layer only one centimetre in thickness. In dog's and pig's bile the spectrum sometimes terminates in the first half of the green, at or just beyond the situation of the line E; and in human bile even within this point, about the commencement of the green part of the spectrum.

Another peculiarity of the spectrum of bile is that its light does not fade away gradually toward the more refrangible portions, as is the case with most other colored fluids, but it terminates suddenly, so that the light is cut off abruptly at the situations above mentioned, thus making a strong contrast with the complete darkness immediately beyond its limits. This peculiarity is perceptible in bile of all shades of green, olive, yellow, or reddish-brown.

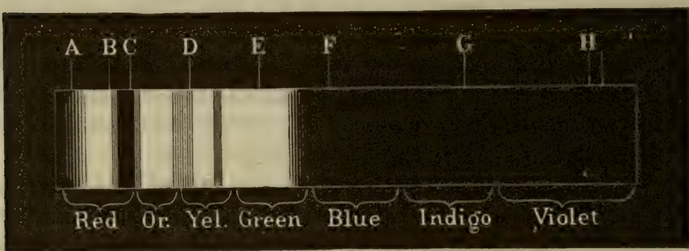
[1] If any colored fluid be placed before the slit of a spectroscope, so that the light which passes through it is afterward dispersed by the prism of the instrument, to form a spectrum, it is found that it absorbs the light of the different colors with different degrees of intensity. When the absorption of light in any particular part of the spectrum is so strong as to cause at that spot a decided dimness in comparison with the neighboring regions, it is called an "absorption band," and is characteristic of the fluid which produces it. The situation of an absorption band is usually indicated by reference to Frauenhofer's lines of the solar spectrum, known as A, B, C, D, E, F, G, and H.

The spectrum of bile shows furthermore three absorption bands, situated in the red, the orange, and the yellow.

The first is a dark and strongly marked band in the red, at the situation of the line C, but extending usually a considerable distance to the left toward B. Its width varies with the thickness of the layer of fluid examined, but when this is increased beyond a certain limit the whole of the red disappears, so that the absorption of light at this spot is no longer visible as a distinct band with red on each side of it. The band itself rarely reaches the situation of the line B, and seldom or never passes beyond it without extinguishing at the same time all the red light of the spectrum. In layers of two or three centimetres' thickness it is quite dark, often almost black, while the red on each side of it is still very brilliant.

As a rule, the intensity of the absorption band at C is in proportion to the preponderance of green in the color of the bile. Though easily seen, in comparatively thin layers, in specimens of a pure green or a decided greenish-olive color, it is less perceptible in specimens of a yellowish, yellowish-brown, or olive-brown tint. But if a specimen of reddish or yellowish-brown bile, which does not show the band distinctly, be turned green by the addition of a few drops of an iodine solution, the band at C at once becomes visible, often to a very marked degree.

Fig. 69.



SPECTRUM OF GREEN (SHEEP'S) BILE.

It would appear from this that the band at C in the spectrum of bile is probably due to the presence of its green rather than its red coloring matter. As the bilirubine is well known to be converted by oxidizing agents into biliverdine, and as this change is accompanied by the appearance of the C band when it was not previously visible, it is evident that the band in question belongs to the green coloring matter. At the same time it is occasionally to be seen in the spectrum of dog's bile which is olive-brown or even brownish-yellow in hue; its intensity in these cases being much increased by turning the bile of a decided green with iodine.

The absorption band at C is a normal characteristic of the bile, and is not dependent on post-mortem changes in the secretion. We have seen it distinctly marked in the spectrum of perfectly fresh sheep's bile,

examined within fifteen minutes after the animal was killed and the gall-bladder taken out of the abdomen.

The two other absorption bands of bile are exceedingly faint in comparison with the first, and much less constant in their occurrence. One of them, very dim and ill-defined, is situated at the junction of the orange and yellow, immediately to the left of the line D, occupying about the last third of the space between C and D. The remaining band is much narrower than either of the others, but a little more distinctly defined than the second. It is situated at about one-third the distance between D and E. The last two absorption bands are more frequently visible in sheep's bile than in that of other animals; but all three may be sometimes seen in a watery solution of desiccated ox-bile which has been kept, in the form of a dry powder, for several years.

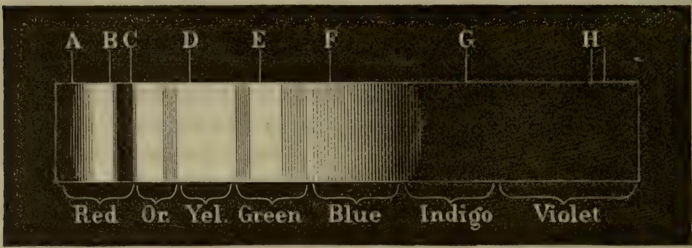
Lastly, the spectrum of bile exhibits a remarkable diminution in intensity of the orange and yellow colors. As the second absorption band is situated at the junction of these colors, it will account for a part of this diminution; but the light of the spectrum is also remarkably dim in the space between the second and third absorption bands, where, in the normal spectrum, it is at the brightest. This is the place naturally occupied by pure yellow, but in the great majority of cases, in the spectrum of bile, there is no pure yellow perceptible, and but little or no orange. The situation of these two colors is encroached upon by the red and green respectively; and in not a few instances, as the spectrum terminates before the commencement of the blue, the only colors really perceptible in it are red and green. The line C in the normal spectrum is situated at the junction of the red and orange, and yet the principal absorption band at this point, when viewed in the spectrum of bile, nearly always appears to be situated entirely in the red, owing to this color taking the place of the orange on the right of the line C. This peculiarity in the spectrum of bile shows itself, whether the color of the specimen be greenish or yellowish-brown.

If a tolerably thick layer of bile be placed before the spectroscope, and the slit of the instrument gradually opened, the first light which appears in the spectrum is a *green* light, in the latter half of the space between D and E. On continuing to increase the size of the opening, if the bile be deeply colored, the next to appear is a *red* light, at the extreme end of the spectrum between A and B; in less concentrated specimens the red light may show itself simultaneously on both sides of the absorption band at C. Afterward the green light extends further toward the left until the spectrum is complete.

The spectrum of bile, in its most important feature, namely, the absorption band at C, presents a remarkable similarity to that of chlorophylle. The band at C is identical in the two spectra so far as regards its position and general appearance; the only perceptible difference being that in an alcoholic solution of chlorophylle its edges are more sharply defined than is usually the case in the spectrum of bile. In other respects, however, the spectrum of chlorophylle differs from that

of bile, since it has three additional absorption bands less distinct than at C, but sufficiently well marked and differently situated from those of bile. One of these additional bands is placed at about three-quarters the distance from C to D, another a little to the left of E, and a third,

Fig. 70.



SPECTRUM OF CHLOROPHYLLE IN ALCOHOLIC SOLUTION.

wider than the others, but very faint and ill-defined, about midway between E and F. In the spectrum of chlorophylle, also, notwithstanding the strong absorption of light at the situation of the principal bands, the yellow of the spectrum appears in its proper place and with nearly its natural hue. An additional distinction of chlorophylle, as compared with that of bile, is that its light does not terminate abruptly, but fades more or less gradually toward the refrangible end.

The bile exhibits a peculiar reaction when treated with *nitric acid*, owing to the effect upon its coloring matter. If a moderate quantity of dilute nitric acid be added to fresh bile and the mixture shaken up, the whole becomes of a bright grass-green, the first color produced by oxidation of the bilirubine and biliverdine. But if the bile be brought in contact, in a cylindrical glass vessel, with a layer of strong nitric acid, especially if it contain a trace of nitrous acid, and allowed to remain without agitation, a series of colored rings are produced at the surface of contact of the two liquids, following each other in a definite order, from the bile to the nitric acid, as green, blue, violet, red, and yellow. These colors represent successive stages of oxidation and final destruction of the biliary coloring matter. The test is known as "Gmelin's bile test," and may be applied to other animal fluids in which bilirubine or its derivatives are supposed to be present.

Composition of the Bile.—In its immediate composition the bile is especially destinguished by the presence of the two peculiar biliary salts, namely, sodium glycocholate and sodium taurocholate, which have been described in Chapter VI., under their appropriate heads. It is evidently these substances which give to the secretion its most important characters. They vary in relative quantity in the bile of different animals, and perhaps also in that of the same species at different times. They are produced, like the coloring matters, in the substance of the liver itself, while other ingredients of the secretion, such as the various min-

eral salts, fatty matters and cholesterine, occur in other parts of the system, and are supplied to the liver, ready formed, in the blood. In the inferior animals, bile can be obtained, for purposes of analysis, in a state of freshness and purity, from the gall-bladder of the recently slaughtered animal; but in man it is usually more or less altered in character by remaining in the gall-bladder for some hours after death. It was obtained in a case of accidental biliary fistula in the human subject by Jacobsen, who found that the entire solid ingredients amounted to about 22.5 parts per thousand; a little over one-third consisting of mineral salts, the remaining two-thirds of organic matters. Sodium glycocholate was invariably present, the taurocholate being less constant; and the fluid always contained both bilirubine and biliverdine. The proportions of all the different ingredients, according to the results of his analyses, were as follows:—

Composition of Human Bile, according to the Analyses of Jacobsen.

	Water	977.40
Organic matters	Sodium glycocholate	9.94
	Cholesterine	0.54
	Free fats	0.10
	Sodium palmitate and stearate	1.36
	Lecithine	0.04
	Other organic matters	2.26
Mineral salts	Sodium chloride	5.45
	Potassium chloride	0.28
	Sodium phosphate	1.33
	Lime phosphate	0.37
	Sodium carbonate	0.93
		1000.00

In ox-bile, as shown by the previous analyses of Berzelius, Frerichs, and Lehmann, the proportion of both mineral and organic ingredients may be very much greater than the above, the biliary salts themselves amounting to 90 parts per thousand. According to Robin[1] they may exist, even in human bile, in the proportion of 56 to 106 per thousand parts.

Tests for the Biliary Salts.—In testing for the existence of bile in other animal fluids, a distinction must be made between those reactions which indicate only the presence of the coloring matters, and those which are appropriate for the detection of the biliary salts proper. The optical properties of bilirubine and biliverdine, already described, and especially the colors produced by the action of nitric acid, constitute a test for these coloring matters alone. They do not indicate the presence of the most essential ingredients of the secretion, which may be contained in an animal fluid unaccompanied by the coloring matters, or, on the other hand, may be absent where the coloring matters are to be

[1] Leçons sur les Humeurs. Paris, 1874, p. 656.

found in appreciable quantity. Other tests are therefore necessary in investigations for the biliary salts proper.

The ordinary characters of the biliary salts are that they are soluble in water and in absolute alcohol, and insoluble in ether; and that they will gradually crystallize in the form of radiating needles, if precipitated from their alcoholic solution by the addition of ether in excess. Furthermore, they are both precipitable from their watery solutions by the tribasic lead acetate, while the sodium glycocholate is also precipitable by the neutral acetate of the same metal.

Pettenkofer's Test.—The biliary salts accordingly, when in considerable quantity, may be recognized by the above-named properties; but when present in smaller proportions they are to be detected by the reaction known as "*Pettenkofer's test.*" This consists in the production of a red color, changing to a purple or violet, on the addition of cane sugar and sulphuric acid. The test is applied in the following way: One part of cane sugar is dissolved in four parts of water. Of this saccharine liquid, one drop is added to each cubic centimetre of the solution of biliary salts. The sugar should not be used in larger quantity, because it might in that case give a perceptible brown tinge under the action of sulphuric acid and heat. The admixture of the sugar produces no visible change in the solution of biliary salts. On adding a few drops of pure sulphuric acid, the biliary acids are decomposed, forming cholic acid. If the biliary salts were originally present in the solution in a proportion of not more than one part in 500, the fluid remains clear; if in larger quantity, the cholic acid is precipitated, forming a whitish turbidity. This turbidity is again cleared up on the continued addition of sulphuric acid; and in the course of a few minutes, a cherry-red color appears, which rapidly changes to a violet, and subsequently, if the biliary salts be present in the proportion of one part in 500, or over, to a deep rich purple. In very dilute solutions, the violet or purple color may not be distinctly visible before the end of an hour.

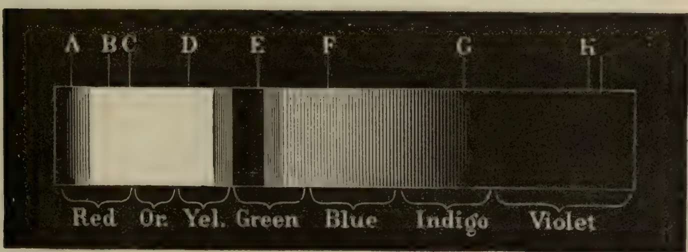
The precautions necessary to observe in using this test are as follows: First, the liquid to be examined should be free from other organic substances, particularly albuminous and coloring matters, which might themselves cause discoloration of the mixture. For this purpose, the suspected fluid should always be first evaporated to dryness, the dry residue extracted with absolute alcohol, the alcoholic solution decolorized, if necessary, with animal charcoal, then precipitated with ether in excess, and the ether precipitate finally dissolved in water. This gives a clear, colorless solution, free from other organic contamination. Secondly, as the liquid becomes heated by the liberal admixture of sulphuric acid with the watery solution, its temperature should not be allowed to rise above 70° (158° F.) nor to fall much below this point. The test-tube may therefore be cooled by occasionally moistening it in cold water. Thirdly, the addition of the sulphuric acid should be made slowly, and should be stopped as soon as a red tint begins to show itself, the mix-

ture being allowed to remain at rest until the violet and purple colors are developed.

There are various other substances which yield a red, violet, or purple color, when treated with sugar and sulphuric acid. Among these are oleine, oleic acid, ethereal oil, amyl-alcohol, albuminous matters and the salts of morphine and codeine. Albumen of the blood, white of egg, and the opium alkaloids in the proportion of ten parts per thousand, if treated with Pettenkofer's test, all produce a color undistinguishable from that obtained with the biliary salts. These substances, however, with the exception of morphine, may all be excluded by previously treating the fluid as above described; namely, evaporating to dryness, extracting with alcohol, precipitating with ether, and dissolving the precipitate in water. The salts of morphine might still remain, as they are soluble both in water and in alcohol, and may be precipitated by ether from their alcoholic solution. This substance, however, is very unlikely to be present in an extract of the animal fluids, especially in the proportion of ten parts per thousand.

Pettenkofer's test is a very delicate one for either or both of the biliary salts. A watery solution of pure sodium glycocholate, made in the proportion of 1 part to 2000, yields, at the end of fifteen minutes, a clear violet pink color, if the test be applied with care; and a solution of sodium taurocholate, in the proportion of 1 part to 3000, will give a similar color at the end of an hour. The general characters of the test are the same in both cases, as the reaction is really produced by cholic acid, derived from the decomposition of either the glycocholic or tauro-cholic acid of the original biliary salts.

Fig. 71.



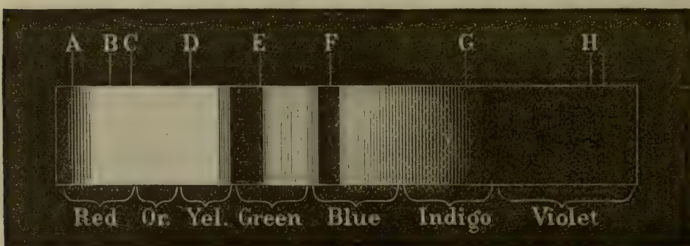
SPECTRUM OF PETTENKOFER'S TEST, with the Biliary Salts in watery solution.

The *spectrum* of Pettenkofer's test presents certain characters which may be of service in distinguishing it from the reactions produced by other organic substances. If either or both of the biliary salts, dissolved in water, be treated with sugar and sulphuric acid until a violet or purple color is produced, and the colored fluid then placed before the slit of the spectroscope, its spectrum shows a wide and dark absorption band at E, extending usually from midway between D and E to a quarter part the distance between E and F, the central parts of the

band being darker than the edges. Beyond the absorption band, the light of the spectrum is dim, fading gradually and terminating somewhere about the line G.

When the purple color produced by Pettenkofer's test with the biliary salts is very pronounced, it is usually found that the fluid is altogether too opaque for spectroscopic examination, even in a layer of only one centimetre. But if it be diluted with water, it becomes turbid, owing to a re-precipitation of cholic acid, and the purple color disappears. This difficulty, however, may be obviated by using a solution of the biliary salts which is sufficiently dilute in the first instance. If sodium glycocholate be dissolved in water, in the proportion of 1 part to 500, and the solution treated with Pettenkofer's test, it gives in a few moments a clear violet-pink color, which afterward becomes a rich purple. This fluid is so opaque that, when placed before the slit of the spectroscope in a layer of one centimetre, it extinguishes completely everything but the red; and yet it may be diluted with water without showing any turbidity or losing its color. A watery solution of this strength is amply sufficient to exhibit the reaction of Pettenkofer's test and the spectroscopic appearances belonging to it. If any solution, therefore, of the biliary salts should prove, on trial, too opaque for spectroscopic examination when treated by Pettenkofer's test, another portion of it may be diluted, before applying the test, until it is reduced to about the strength of 1 part to 500. Even when a strongly colored purple fluid has been rendered turbid and decolorized by the addition of water, its transparency and color may be again restored by the addition of sulphuric acid; but this method is less convenient than the former.

Fig. 72.



SPECTRUM OF PETTENKOFER'S TEST, with the Biliary Salts in alcoholic solution.

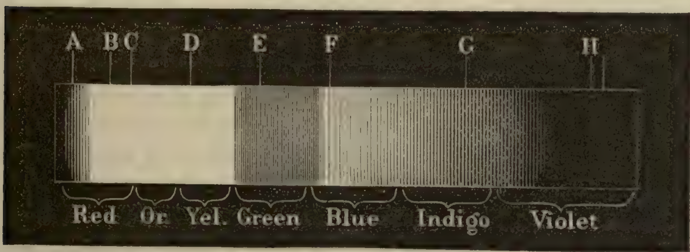
If Pettenkofer's test be applied to the biliary salts in alcoholic solution, its spectrum is modified. There are now two absorption bands instead of one. The first is situated at E, and is identical with that obtained in a watery solution of the same salts. The second is at F, and usually rather narrower and fainter than the first, although sometimes the two bands are of equal intensity.

The pink or purplish-red fluid, produced by Pettenkofer's test with

both codeine and morphine, has a spectrum very similar to that of the biliary salts. If the ruddy color of the fluid be strongly pronounced, its spectrum, even when viewed in a layer of one centimetre, is very short, terminating completely about midway between D and E, or even before that point, showing the red and yellow clear and bright, but very little of the green. If diluted with water, the mixture is not rendered turbid, but its color is very much reduced, being soon changed to a faint amber or often to a light apple-green, while the former peculiarities of the spectrum disappear. The best way is to place the fluid before the slit of the spectroscope in a layer of two centimetres before its color is fully developed, and while it is still of a light pink. The color then gradually becomes more pronounced, and, when it has attained the proper degree of strength, the spectrum exhibits a certain though ill-defined absorption-band at E. Beyond the band, the whole spectrum is very dim, and terminates gradually between F and G.

The distinction between the spectrum of Pettenkofer's test with biliary salts and that with the opium alkaloids is, that in the former case the absorption-band at E is very marked and distinct, and often quite black, when viewed in a layer of two centimetres' thickness, while in the latter it is always dim and very ill-defined. With the biliary salts, also, the fluid may frequently be diluted with its own or even twice its volume of water, and the absorption-band still remain plainly visible; but with morphine or codeine a very moderate dilution rapidly destroys the character of the spectrum and causes the absorption-band to disappear.

Fig. 73.



SPECTRUM OF PETTENKOFER'S TEST, with albumen.

The violet-colored fluid produced by Pettenkofer's test with albumen has a well-marked and peculiar spectrum, easily distinguishable from that belonging to the biliary salts. If tolerably dense, it requires to be diluted with water for spectroscopic examination, and afterward cleared up by the further addition of sulphuric acid. The spectrum then shows a single absorption-band, extending from somewhere about the line E to the line F, and occupying the intermediate space. In concentrated specimens it may begin considerably to the left of E, and extend thence to F. If the albuminous liquid be more dilute, it may reach only from

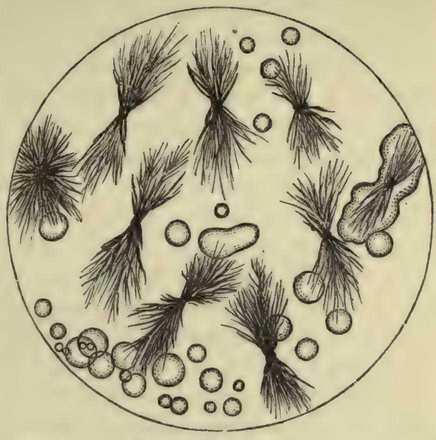
a short distance beyond E to F. It is, therefore, always limited on the right by the line F, but extends farther toward E and D, according to the degree of concentration of the liquid. Its edges are not very well defined, but are more distinct when the band is narrow than when it is wide. Beyond the band, the refrangible portion of the spectrum is quite dim.

Mode of Secretion of the Bile.—It is a matter of importance, in regard to the bile, as well as the other intestinal fluids, to ascertain whether it be a *constant* secretion, like the urine and perspiration, or whether it be *intermittent*, like the gastric juice, and discharged only during the digestive process. Bidder and Schmidt have investigated this point in the following manner: They operated by tying the common bile-duct, and then opening the fundus of the gall-bladder, so as to produce a biliary fistula, by which the whole of the bile was drawn off. By doing this operation, and collecting and weighing the fluid discharged at different periods, they came to the conclusion that the flow of bile begins to increase within two and a half hours after the introduction of food into the stomach, but that it does not reach its maximum of activity till the end of twelve or fifteen hours. Other observers, however, have obtained different results. Arnold,[1] for example, found the quantity to be largest soon after meals, decreasing again after the fourth hour. Kölliker and Müller,[2] again found it largest between the sixth and eighth hours. It appears, accordingly, that the bile is not an intermittent but a constant secretion; and that the quantity produced varies with the condition of the digestive process, being, according to the majority of observers, most abundant some time after the digestion and absorption of food have commenced in the intestinal canal.

Discharge of Bile into the Intestinal Canal.—As, in those animals which have been the subject of experiment, the liver is provided with a gall-bladder, in which the secretion may be partially accumulated after its production, and from which it may find its way at regular or irregular intervals into the alimentary canal, it becomes important to ascertain by other means at what time and in what quantity it is really discharged into the intestine. In order to determine this point, we have performed the following series of experiments on dogs. The animals were kept confined, and killed at various periods after feeding, sometimes by the inoculation of woorara, sometimes by hydrocyanic acid, but most frequently by section of the medulla oblongata. The contents of the intestine were then collected and examined. In all instances, the bile was also taken from the gall-bladder and treated in the same way, for purposes of comparison. The intestinal contents always presented some peculiarities of appearance when treated with alcohol and ether, owing probably to the presence of other substances than the bile; but they always gave evidence of the presence of biliary matters as well. The

[1] Cited in the American Journal of the Medical Sciences, April, 1856.
[2] Ibid., April, 1857.

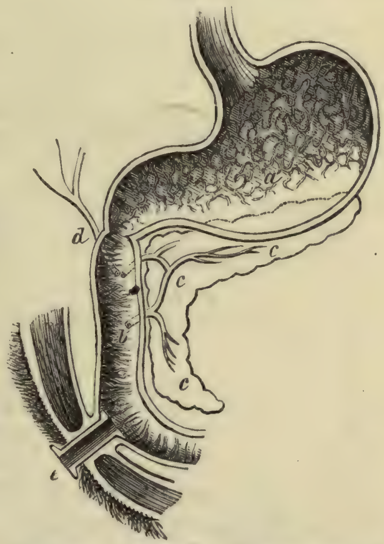
Fig. 74.



Crystalline and Resinous Biliary Substances; from Small Intestine of Dog, after two days fasting.

biliary substances could almost always be recognized by the microscope in the ether precipitate of the alcoholic solution; both as a resinous matter, under the form of rounded, oily-looking drops (Fig. 74), and also under the form of crystalline groups, generally presenting the appearance of double bundles of slender, radiating, slightly curved or wavy, needle-shaped crystals. These substances, dissolved in water, gave a purple color with sugar and sulphuric acid. These experiments were tried after the animals had been kept for one, two, three, five, six, seven, eight, and twelve days without food. The result showed that, in all these instances, bile was present in the small intestine. The bile, therefore, is not only constantly secreted by the liver in the intervals of digestion, as well as during that process, but it also continues to be discharged into the intestine for many days after the animal has been deprived of food.

Fig. 75.



Duodenal Fistula.—*a.* Stomach. *b.* Duodenum. *c, c, c.* Pancreas; its two ducts are seen opening into the duodenum, one near the orifice of the biliary duct, *d*, the other a short distance lower down. *e.* Silver tube passing through the abdominal walls and opening into the duodenum.

But the quantity of bile passing into the intestine within a given time is greatest soon after the commencement of digestion. Our own experiments bearing on this point were performed on dogs, by making a permanent duodenal fistula, on the same plan as that used for gastric fistulæ (Fig. 75). An incision was made through the abdominal walls, a short distance to the right of the median line, the floating portion of the duodenum drawn up toward the external wound, opened by a longitudinal incision, and a silver tube, armed at each end with a narrow projecting flange, inserted into it by one extremity, about fourteen centimetres below the pylorus, and seven centimetres

below the orifice of the lower pancreatic duct. The other extremity of the tube was left projecting from the external opening in the abdominal parietes, the parts secured by sutures, and the wound allowed to heal. After cicatrization was complete, and the animal had entirely recovered his healthy condition and appetite, the intestinal fluids were drawn off at various intervals after feeding, and their contents examined. This operation, which is rather more difficult than that of making a permanent gastric fistula, is nevertheless exceedingly useful when it succeeds, since it enables us to study the actual time and rate of the biliary discharge into the upper part of the intestinal canal.

In order to ascertain the absolute quantity of bile discharged into the intestine, and its variations during digestion, the duodenal fluids were drawn off, for fifteen minutes at a time, at various periods after feeding, collected, weighed, and examined separately, as follows: each separate quantity was evaporated to dryness, its dry residue extracted with absolute alcohol, the alcoholic solution precipitated with ether, and the ether-precipitate, regarded as representing the amount of biliary salts present, dried, weighed, and then treated with Pettenkofer's test, in order to determine, as nearly as possible, their degree of purity or admixture. The result of these experiments is given in the following table. At the eighteenth hour so small a quantity of fluid was obtained that the amount of its biliary ingredients was not ascertained. It reacted perfectly, however, with Pettenkofer's test, showing that bile was really present.

Discharge of Intestinal and Biliary Fluids from Duodenal Fistula in a Dog Weighing 16.5 Kilogrammes.

Time after feeding.	Quantity of fluid in 15 minutes.	Dry residue of the same.	Quantity of biliary salts.	Proportion of biliary salts in the dry residue.
	(Grammes.)	(Grammes.)	(Grammes.)	(Per cent.)
Immediately.	41.467	2.138	0.648	30
1 hour.	128.936	6.803	0.259	3
3 hours.	50.537	3.887	0.259	7
6 "	48.594	4.729	0.227	5
9 "	55.721	5.053	0.291	6
12 "	21.057	1.490	0.243	16
15 "	22.482	1.166	0.259	22
18 "	—	—	—	—
21 "	24.880	0.712	0.064	9
24 "	10.561	0.615	0.210	34
25 "	9.783	0.324	0.194	60

From this it appears that the bile passes into the duodenum in by far the largest quantity immediately after feeding. This is undoubtedly due to a contraction of the gall-bladder and a discharge of the surplus bile accumulated in it during the interval of digestion. It is a matter of common observation that the gall-bladder, in animals killed after a day or two of fasting, is distended with an unusual quantity of thick and dark-looking bile; while in those killed immediately or soon after

feeding, it is comparatively collapsed and empty. This evacuation of the gall-bladder, excited by the ingestion of food, causes a sudden flow of bile into the duodenum. After that time, its discharge remains pretty constant; not varying much, in a dog of sixteen and a half kilogrammes' weight, from 256 milligrammes of the biliary salts every fifteen minutes, or a little over one gramme per hour. In a man of ordinary size (65 kilogrammes), if the quantity of bile were increased in proportion, this would amount to 8.667 grammes of solid biliary matter per hour discharged into the intestine during the greater part of the digestive process.

Daily Quantity of the Bile.—The first experiments of value upon this point were those of Bidder and Schmidt, published in 1852.[1] They were performed upon dogs, cats, sheep, and rabbits, in the following manner: The abdomen was opened, and a ligature placed upon the common biliary duct, so as to prevent the bile finding its way into the intestine. An opening was then made in the fundus of the gall-bladder, by which the bile was discharged externally. The bile, so discharged, was received into previously weighed vessels, and its quantity accurately determined. Each observation usually occupied about two hours, during which period the temporary fluctuations occasionally observable in the quantity of bile discharged were mutually corrected, so far as the entire result was concerned. The animal was then killed, weighed, and carefully examined, in order to make sure that the biliary duct had been securely tied, and that no inflammatory alteration had taken place in the abdominal organs. The observations were made at different periods after the last meal, so as to determine the influence exerted by the digestive process upon the rapidity of the secretion. The average quantity of bile for twenty-four hours was then calculated from a comparison of the above results; and the quantity of its solid ingredients was also ascertained in each instance by evaporating a portion of the bile in the water bath, and weighing the dry residue.

Bidder and Schmidt found in this way that the daily quantity of bile varied considerably in different species of animals. It was much greater in the herbivorous animals used for experiment than in the carnivora. The results obtained by these observers were as follows:

For every kilogramme of the entire bodily weight of the animal, there is secreted, in twenty-four hours,

	Fresh bile.	Dry residue.
In the cat . . .	14.537 grammes.	0.816 grammes.
" dog . . .	19.956 "	0.985 "
" sheep . . .	25.372 "	1.340 "
" rabbit . . .	136.556 "	2.464 "

According to the later researches of Schiff,[2] these estimates are certainly not beyond the truth, since he obtained considerably larger quantities in the dog, by simply establishing an open fistula of the gall-

[1] Verdauungssaefte und Stoffwechsel. Leipzig, 1852.
[2] Archiv für die Gesammte Physiologie. Bonn, 1870, Band iii. p. 598.

bladder, without tying the common biliary duct. While the average quantity obtained in Bidder and Schmidt's experiments on the dog was 0.832 grammes of fresh bile per hour for every kilogramme of bodily weight, in those of Schiff it was 1.3 to 3.2 grammes per kilogramme per hour.

Since in the human subject the processes of digestion and nutrition resemble those of the carnivora, rather than those of the herbivora, the former should be selected to serve as a term of comparison in estimating the probable daily quantity of the bile in man. If we apply accordingly to the human subject the average of the results obtained by Bidder and Schmidt from the cat and dog, the entire quantity of bile, for a man weighing 65 kilogrammes, would be a little over 1100 grammes per day. Ranke[1] obtained from direct observation a result not essentially different from this. He collected at various times the bile discharged in a case of biliary fistula in a man weighing only 47 kilogrammes, and found the average quantity for twenty-four hours to be 652 grammes; the maximum quantity for the same period being 945 grammes. In a man of 65 kilogrammes' weight this would correspond, for the average, to 902 grammes, and for the maximum to 1307 grammes. The entire quantity of bile, therefore, for a man of medium size, is evidently not far from 1000 grammes per day. This contains about 30 grammes of solid ingredients.

Decomposition of the Biliary Matters in the Intestine.—Observers generally are agreed that the biliary salts, though constantly poured into the upper part of the intestinal canal, are not discharged with the feces. Although traces of them are sometimes to be found in the evacuations, they are always very far from representing the total quantity produced by the liver, and as a general rule they disappear altogether in their passage through the intestine. This may be readily demonstrated by experiments upon dogs, which are conducted in the following manner. The animals are to be fed with fresh meat, and then killed at various intervals after the meals, the abdomen opened, ligatures placed upon the intestine at various points, and the contents of its upper, middle, and lower portions collected and examined separately. The results thus obtained show that, under ordinary circumstances, the bile, which is quite abundant in the duodenum and upper part of the small intestine, diminishes in quantity from above downward, and is not to be found in the large intestine. The entire quantity of the intestinal contents also diminishes and their consistency increases, as we approach the ileo-cæcal valve; and at the same time their color changes from a light yellow to a dark bronze or blackish-green, which is always strongly pronounced in the last quarter of the small intestine.

If the contents of the small and large intestine be furthermore evaporated to dryness, extracted with absolute alcohol, and the alcoholic solutions precipitated with ether, the quantity of ether-precipitate being

[1] Grundzüge der Physiologie des Menschen. Leipzig, 1872, p. 284.

regarded as representing approximately that of the biliary substances proper, the result shows that the quantity of ether-precipitate is, both positively and relatively, very much less in the large intestine than in the small. Its proportion to the entire solid contents is only one-fifth or one-sixth as great in the large intestine as it is in the small. But even this inconsiderable quantity, found in the contents of the large intestine, does not consist of biliary matters; for, the watery solutions being treated with sugar and sulphuric acid, those from both the upper and lower portions of the small intestine always give Pettenkofer's reaction perfectly in less than a minute and a half; while in that from the large intestine no red or purple color is usually produced, even at the end of three hours.

The small intestine consequently contains, at all times, substances presenting the usual reactions of the biliary ingredients; while in the contents of the large intestine no such substances can be recognized by Pettenkofer's test.

It is not possible to say, however, what is the precise nature of the changes undergone by the biliary salts in the intestinal canal. The supposed decomposition of these salts by contact with the acid secretions of the alimentary canal, and the separation of the glycine, taurine, and cholic acid of their organic ingredients, with their subsequent transformations, are all more or less hypothetical, and without sufficient basis of experimental evidence. The biliary matters in the intestine pass, by decomposition or metamorphosis, into the condition of other unknown substances which do not respond to Pettenkofer's test.

Physiological Function and Destination of the Bile.—The physiological function of the bile is still very obscure. With regard to its action in the digestive process, we may say that nothing whatever is yet known which can account for the constant presence of so important and peculiar a secretion. By itself, in experiments on artificial digestion, it does not exhibit any direct action upon either of the principal alimentary substances, of such a definite character as those which belong to the gastric, pancreatic, and intestinal juices; its action being limited to simple solution of a certain proportion of oily matter, and to a feeble and inconstant transforming power upon hydrated starch. Two other actions have also been attributed to it, from certain properties which observation shows it to possess; namely, first, that of exciting the secretions and peristaltic movement of the intestine and thus serving as a natural cathartic, and secondly, that of facilitating the absorption of oily matters by the intestinal mucous membrane. But although the bile is found, when applied to the muscular coat of the intestine, to excite its contraction, and similar effects are thought to have been seen even in the villi, yet the alimentary canal is known to be naturally excited to action by the ingestion of food, or its downward passage from other parts; and there is nothing to show that the intestine, below the orifice of the biliary duct, should require any peculiar or exceptional stimulus for the excitement of its normal actions. It is true, in the second place, that the bile

has been shown, by direct experiment, to facilitate the passage of oily matters by osmosis through closed organic membranes or parchment paper; that is, oily matters will pass through these membranes more readily when they are moistened with bile, than when simply wetted with water; and it is upon these experiments that the supposed function of the bile, in effecting the absorption of oil in the intestine, has been based. But the villi of the intestine are not simply membranes moistened with water. They are penetrated throughout by alkaline and albuminous fluids, their bloodvessels contain an abundance of organic material in the liquid form, and the fatty emulsion formed by the pancreatic juice is itself fully adapted for absorption by the villi. There seems to be no good reason for assigning to the physical properties of the bile, in this respect, any special importance for the absorption of fatty substances.

An action of quite the opposite nature has also been attributed to the bile, namely that of precipitating the half-digested ingredients of the food from their solution in the gastric juice. But there is reason to believe that this also rests upon an error, and that there is no such antagonism between the bile and the gastric juice in the intestine as when they are mingled together in a test-tube.

It has already been stated (page 159) that the bile precipitates by contact with the gastric juice. If one or two drops of dog's bile be added to as many cubic centimetres of fresh gastric juice from the same animal, a copious yellowish-white precipitate falls down, containing the whole of the coloring matter of the bile which has been added; and if the mixture be then filtered, the filtered fluid passes through quite colorless. The gastric juice, however, still retains its acid reaction. This precipitation depends upon the presence of the biliary substances proper, namely, the sodium glycocholate and taurocholate; for if the bile be evaporated to dryness and the biliary substances extracted by alcohol and precipitated by ether in the usual manner, their watery solution will precipitate with gastric juice, in the same way as fresh bile would do.

Although the biliary matters, however, precipitate by contact with fresh gastric juice, *they do not do so with gastric juice which holds albuminose in solution.* We have invariably found that if the gastric juice be digested for several hours at the proper temperature with boiled white of egg, the filtered fluid, which contains an abundance of albuminose, will no longer give the slightest precipitate on the addition of bile or of a watery solution of the biliary substances, even in very large amount. The gastric juice and the bile, therefore, are not finally incompatible with each other in the digestive process, notwithstanding the reaction which takes place between them when artificially mingled.

Although, however, the bile cannot be shown to exert any direct action in the digestion of the food, similar to that of the other intestinal fluids, yet there is evidence that it takes part, in the intestine, in some process which is important, and even, in the long run, essential to life. This is shown by the fact that if the bile be permanently diverted from

the cavity of the intestine by closure of the common bile-duct, and evacuated by a fistula of the gall-bladder, the animals which are the subjects of the operation gradually emaciate, and die with general symptoms of disordered nutrition.

This experiment has been successfully performed at least ten times by Schwann, Bidder and Schmidt,[1] Bernard,[2] and Prof. A. Flint, Jr.,[3] the animals surviving the immediate effects of the operation, the biliary fistula remaining open, and the common bile-duct, as shown by subsequent *post-mortem* examination, being permanently closed so that none of the bile could have found its way into the intestine. The general results were alike in these cases. The animals died with the signs of inanition, usually between 30 and 40 days after the operation; although in one instance death occured at the end of the seventh day, and in another not until the eightieth. The average length of life, in all the cases taken together, was 36 days. The symptoms were constant and progressive emaciation, which proceeded to such a degree that nearly every trace of fat disappeared from the body. The loss of flesh amounted, in one case, to more than two-fifths, and in another to nearly one-half the entire weight of the animal. There was also sometimes a falling off of the hair, and an unusually disagreeable, putrescent odor in the feces and in the breath. Notwithstanding this, the appetite remained good. Digestion was not essentially interfered with, and none of the food was discharged with the feces; but there was, in the cases of Bidder and Schmidt, much rumbling and gurgling in the intestines, and abundant discharge of flatus, more strongly marked in one instance than in the other. There was no pain; and death took place, at last, without any violent symptoms, but by a simple and gradual failure of the vital powers.

It appears therefore that the bile is not simply an excrementitious fluid destined to be eliminated from the system; but that, after being secreted and discharged by the liver, it must pass into and through the small intestine, in order to maintain the continuous and healthy nutrition of the body. We have already seen, furthermore, that its most essential ingredients, namely, the biliary salts, disappear during their passage through the alimentary canal, and are not to be found in the fecal evacuations. This may be accounted for in two different ways. Either the biliary salts, while in the intestine, may become altered and insoluble, so as to lose their reaction with Pettenkofer's test, and be finally evacuated with the feces under this insoluble form; or, on the other hand, they may be reabsorbed from the alimentary canal and thus re-enter the circulation as ingredients of the blood.

The conclusion generally adopted by physiologists is that they are reabsorbed. The most positive evidence on this point is that derived

[1] Verdauungssaefte und Stoffwechsel. Leipzig, 1852, p. 103.

[2] Liquides de l'Organisme. Paris, 1859, tom. ii. p. 199.

[3] Physiology of Man. New York, 1867, p. 369.

from the experiments of Bidder and Schmidt on the quantity of sulphur contained in the feces of the dog, as compared with that in the taurocholic acid of his biliary salts. The significance of these experiments depends upon the fact that the biliary salts themselves, being compound bodies, might be so altered by decomposition in the intestine as to lose their characteristic reactions, and yet their separated materials might remain; but as sulphur, on the other hand, is a chemical element, not decomposable by any known means, it must be capable of detection, if present, by ultimate analysis. The dog was selected as the subject of experiment, for the reason that the bile in this animal contains so large a proportion of the sodium taurocholate, of which sulphur is a constituent part.

The results obtained by Bidder and Schmidt[1] showed that the quantity of sulphur evacuated in the feces was much less than that discharged into the intestine with the bile.

These observers collected and analyzed all the feces passed, during five days, by a healthy dog, weighing 8 kilogrammes. The entire fecal mass during this period weighed 97.716 grammes,

Containing	Water	56.642 grammes.
	Solid residue	41.074 "
		97.716

The solid residue was composed as follows:—

Neutral fat, soluble in ether . .	2.832 grammes.	
Fat, with traces of biliary matter .	4.991 "	
Alcohol extract, with biliary matter	3.816	containing 0.070 of sulphur.
Substances not of a biliary nature extracted by muriatic acid and hot alcohol	9.641	containing 0.085 of sulphur.
		0.155
Fatty acids with oxide of iron .	6.377	
Residue consisting of hair, sand, etc.	13.417	
	41.074	

As it has already been shown (page 219) that the dog secretes, during 24 hours, 0.985 gramme of solid biliary matter for every kilogramme of bodily weight, the entire quantity of biliary matter secreted in five days by the above animal, weighing 8 kilogrammes, must have been 39.4 grammes, or nearly as much as the whole weight of the dried feces. But furthermore, the natural proportion of sulphur in dog's bile, derived from the sodium taurocholate, is 6 per cent. of the dry residue. The 39.4 grammes of dry bile, secreted during five days, contained, therefore, 2.364 grammes of sulphur. But the entire quantity of sulphur, existing in any form in the feces, was 0.385 gramme; and of this only 0.155 gramme could have been the product of biliary matters—the re-

[1] Verdauungssaefte und Stoffwechsel. Leipzig, 1852, p. 217

mainder being derived from the hairs which are always contained in abundance in the feces of the dog. That is, not more than one-fifteenth part of the sulphur originally present in the bile could be detected in the feces. It must, accordingly, have been reabsorbed from the intestine.

A still further corroboration of the reabsorption of the biliary materials from the intestinal canal is furnished by the very careful and ingenious experiments of Schiff,[1] performed in a different manner. This observer found that, in animals provided with a gall-bladder, less pressure is required to make a fluid pass from the hepatic duct into the cavity of the gall-bladder than to force it through the common duct into the intestine. Unless, therefore, the pressure under which the bile is secreted be increased, either by distension or by muscular contraction, it passes into the gall-bladder more readily than into the intestine; and a fistula of the fundus of the gall-bladder, if kept freely open, will be of itself sufficient to discharge all, or nearly all, the secreted bile, without any considerable portion of it reaching the intestine. He demonstrated furthermore that this was really the fact by establishing at the same time, in the same animal, a fistula of the gall-bladder and one of the duodenum. So long as the cystic fistula remained open, either no biliary matters, or only insignificant traces of them, could be detected in the fluids drawn from the duodenum.

The advantage, for certain purposes, of this method of operating, over that in which the common duct is also tied and obliterated, is that by the last operation the bile is permanently shut off from the intestine, in consequence of which the animal soon passes into an abnormal and enfeebled condition. One of the earliest results of this unhealthy state is a *diminution in the daily quantity of bile secreted.* On the other hand, by Schiff's method, so long as the cystic fistula is closed, the bile continues to pass through the common duct into the intestine, thus maintaining the animal in a healthy condition. At any time, however, by opening the cystic fistula and emptying the gall-bladder, the rate at which the bile is secreted may be observed with facility. It has already been mentioned that larger quantities of bile were usually obtained by this than by the older method.

The observations of Schiff show that by leaving open the cystic fistula, and thus practically diverting all the bile from the intestine, its rate of secretion by the liver is at once diminished, so that even at the end of twenty-four hours, if the influence of digestion be eliminated, it is already reduced to a minimum, and this minimum continues afterward with only insignificant fluctuations. On the other hand, if, in the same animal, the fistula be kept closed for some hours, the quantity of bile soon rises to its normal standard.

The same observer experimented upon the dog with similar results by making a duodenal fistula, through which he introduced a canula into the orifice of the common bile-duct. This canula had a lateral opening

[1] Archiv für die Gesammte Physiologie. Bonn, 1870, p. 598.

near its inner end, which might be left open or kept closed by shifting the position of an inner tube fitting closely in the canula. Thus the bile might be at will either discharged externally from the orifice of the canula, or allowed to pass into the duodenum by its lateral opening. It was found that, after being discharged externally for even two or three hours previously to the examination, its rate of secretion was much less than if it had been allowed to pass into the intestine. The results obtained, in a dog weighing 12 kilogrammes, were as follows:

CUBIC CENTIMETRES OF BILE OBTAINED IN TEN MINUTES AFTER HAVING BEEN, FROM TWO TO THREE HOURS,

	Evacuated externally.	Discharged into the duodenum.
	2.2	6.0
	2.3	5.4
	2.1	5.6
	2.0	6.2
	1.8	6.5
	1.9	5.7
Average . . .	2.05	5.90

Thus the quantity of bile secreted, when it has been allowed to follow its natural course into the duodenum, is nearly three times as great as when it has been evacuated through the external fistula. It does not necessarily follow from this that it is again directly used for secretion by the liver, since this process may be influenced by a variety of secondary conditions; but it is difficult to avoid the conclusion that its ingredients are absorbed from the intestinal cavity, and supply in some way the materials for continued secretion.

Before their reabsorption, however, the biliary salts undergo certain alterations in the alimentary canal, so that when finally taken up by the bloodvessels, they have already assumed a different form; otherwise they could be detected in the blood of the portal vein. But such researches have constantly led to a negative result. Our own experiments on this point were performed on dogs, by examining the portal blood obtained at different periods after feeding. The animals were killed by section of the medulla oblongata, a ligature immediately placed on the portal vein, while the circulation was still active, and the requisite quantity of blood collected by opening the vein. The blood was sometimes immediately evaporated to dryness by the water-bath. Sometimes it was coagulated by boiling in a porcelain capsule over a spirit lamp, with water and an excess of sodium sulphate, and the filtered watery solution afterward examined. But most frequently the blood, after being collected from the vein, was coagulated by the gradual addition of three times its volume of alcohol, stirring the mixture constantly, so as to make the coagulation gradual and uniform. It was then filtered, the moist mass remaining on the filter subjected to strong pressure in a linen bag, by a porcelain press, and the fluid thus obtained added to that previously filtered. The entire spirituous solution was then evaporated

to dryness, the dry residue extracted with absolute alcohol, and the alcoholic solution treated as usual to discover the presence of biliary matters. In every instance, blood was taken at the same time from the jugular vein, or the abdominal vena cava, and treated in the same way for purposes of comparison.

We have examined the blood, in this way, one, four, six, nine, eleven and a half, twelve, and twenty hours after feeding. The result shows that in the venous blood, both of the portal vein and of the general circulation, there exists a substance soluble in water and in absolute alcohol, and precipitable by ether from its alcoholic solution. This substance is often considerably more abundant in the portal blood than in that taken from the general venous system. It adheres closely to the sides of the glass vessel after precipitation, so that it is always difficult, and often impossible, to obtain enough of it, mixed with ether, for microscopic examination. It dissolves, also, like the biliary substances, with great readiness in water; but in no instance have we ever been able to obtain from it such a reaction with Pettenkofer's test, as would indicate the presence of bile. This is not because the reaction is masked by any other ingredient of the blood; for if, at the same time, a little bile be added to blood taken from the abdominal vena cava, in the proportion of one drop of bile to seven or eight cubic centimetres of blood, and the two specimens treated alike, the ether-precipitate may be considerably more abundant in the case of the portal blood; and yet that from the blood of the vena cava, dissolved in water, will give Pettenkofer's reaction for bile perfectly, while that of the portal blood will give no such reaction.

Notwithstanding the evidence, therefore, that the biliary matters are absorbed by the portal blood, they cannot be recognized there by Pettenkofer's test. They must accordingly have passed through such changes, in the intestine, previously to their absorption, that they can no longer give the ordinary reaction of the biliary salts. We cannot say precisely what these changes are, but they are undoubtedly dependent upon the action of the intestinal juices, and are therefore more rapid while the process of digestion is going on. This is probably the explanation of the fact that the bile, though a continuous secretion, is discharged into the alimentary canal in greatest abundance immediately after the ingestion of food; since it is not so much needed to assist the intestinal juices in the process of digestion, as to be itself acted on by them and converted into other materials.

The bile, accordingly, is a secretion which has not yet accomplished its function when it is discharged from the liver and poured into the intestine. While in the cavity of the alimentary canal, in contact with its glandular surface, and mingled with the intestinal juices, its ingredients lose their original character and pass into the form of new combinations. These substances again enter the circulation by absorption from the intestinal cavity, and are carried away by the blood, to complete their function in some other part of the body.

CHAPTER XI.

PRODUCTION OF GLYCOGEN AND GLUCOSE IN THE LIVER.

If the liver of a carnivorous or herbivorous animal, after twenty-four hours' fasting, be taken from the body immediately after death, finely divided, and boiled for a few moments in water with animal charcoal or an excess of sodium sulphate, to eliminate the albuminous and coloring matters, the filtered fluid will be nearly clear, or show only a moderately opaline tinge. But if the same thing be done within a few hours after the ingestion of animal or vegetable food, the watery decoction of the liver tissue will be strongly opalescent, being rendered turbid by the presence in considerable quantity of a matter which communicates to the solution a partial turbidity. This matter is *glycogen*, which is contained, in greater or smaller quantity, in the liver extract under these two conditions.

This substance, first discovered by Bernard, has so strong an analogy, in its composition and properties, with the ordinary amylaceous matter of vegetable tissues, that it is often spoken of as "animal starch." It is, when purified, a non-nitrogenous body, having the formula $C_6H_{10}O_5$. It is accordingly a carbohydrate, and indentical with starch in its ultimate chemical composition.

It is obtained from the liver by first cutting the organ into small pieces and immediately coagulating them by a short immersion in boiling water. This is for the purpose of prevening the partial transformation of the glycogen which would otherwise take place, under the influence of a moderate temperature, by contact with the albuminous matters present in the liver. These albuminous matters having been once coagulated by the preliminary boiling, the glycogen can afterward be extracted at leisure. The liver tissue is then ground to pulp in a mortar and boiled continuously for half an hour with a small quantity of water, just sufficient to keep the mixture fluid, in order to obtain a decoction as concentrated as possible. The decoction is then treated with animal charcoal, to remove the coloring matters, and filtered. The solution is distinctly opaline, and if allowed to fall into a vessel of strong alcohol, the glycogen, which is insoluble in this fluid, is precipitated in the form of a white deposit. This deposit is still contaminated by a little glucose, and by a certain quantity of biliary salts and other nitrogenous matters. The glucose and biliary salts are removed by repeatedly washing the precipitate with alcohol. The deposit is then boiled for a quarter of an hour with a concentrated solution of potassium hydrate,

which dissolves the albuminous matters, but does not affect the glycogen. After being separated by filtration it is again dissolved in water, the traces of alkali removed by the addition of a little acetic acid, and the glycogen then precipitated anew, in a pure form, by alcohol in excess. It is then dried and may be kept in the form of a white pulverulent mass, which retains its properties for an indefinite time.

Glycogen thus prepared is soluble in water, its solution having an opalescent tinge. Treated with iodine, it gives a violet color, intermediate between the blue reaction of starch and the red of dextrine. It does not reduce the copper salts in Trommer's test, nor give rise to fermentation with yeast; but it is converted into dextrine and glucose by all those agencies which have a similar effect upon starch—namely, prolonged boiling with dilute mineral acids, the contact of vegetable diastase, of saliva, the pancreatic juice, and the serum of blood at a moderately warm temperature. If allowed to remain in the liver after death, a part of it suffers transformation into glucose by contact with the fluids of the hepatic tissue.

Origin and Mode of Formation of Glycogen.—As this substance is present in the liver tissue of both carnivorous and herbivorous animals, it may be derived from the materials of either kind of food. In the carnivora, at least, there is evidence that it is supplied from nitrogenous materials, by the nutritive changes which they undergo in the substance of the liver. Under some circumstances a material resembling glycogen, or identical with it, may be present in the muscles of the herbivora. Bernard has found it in the muscular tissue in rabbits, and especially in pigeons, when fed upon the cereal grains, and in horses kept upon oats and barley; but in all these animals it disappears when the food is changed, or after some days' fasting. Luchsinger[1] has also found it to be absent from the muscles of the rabbit after several days' fasting, but to continue more persistently in the pectoral muscles of the fowl under similar conditions.

It is accordingly not a constant but only an occasional ingredient of muscular flesh, and when present is usually found in very small quantity. Poggiale,[2] in very many experiments instituted for this purpose by a Commission of the French Academy of Sciences, found glycogen present in ordinary butcher's meat only once. We have also found it to be absent from the fresh meat of the bullock's heart, when examined in the manner described above. Nevertheless, in dogs fed exclusively for eight days upon this food, glycogen may be abundant in the liver, while it does not exist in the other internal organs, as the spleen, lungs, and kidneys.

The production of glycogen from nitrogenous substances is also shown, according to Bernard, by the fact that it makes its appearance

[1] Archiv für die Gesammte Physiologie, 1873. Band viii. p. 290.

[2] Journal de la Physiologie. Paris, 1858, p. 558.

in the bodies of maggots during the course of their development, although neither the eggs from which they are hatched, nor the putrefying meat upon which they feed, contain any appreciable traces of this substance.

Glycogen is produced, however, in especial abundance in the liver, after the ingestion of starchy and saccharine food. Bernard[1] found the decoction of the liver tissue in the dog, after feeding for two days with bread and starch paste, very turbid and milky in appearance. Subsequent experiments by the same observer[2] have shown that a starchy diet augments notably the quantity of glycogen existing in the liver. This fact was first demonstrated in a special manner by the observations of Pavy,[3] who, by comparative experiments upon dogs fed with animal and vegetable food, found that the influence of the latter was to increase very decidedly the weight of the whole liver, and also the pencentage of glycogen which it contained. The same effect was produced by a diet of animal food with sugar in addition. The following table gives the average results of three series of observations by Pavy:

AVERAGE PRODUCTION OF GLYCOGEN, IN DOGS, UNDER DIET OF ANIMAL AND VEGETABLE FOOD.

Diet for several days previously.	Weight of liver, in percentage of bodily weight.	Glycogen in the fresh liver, per cent.
Tripe	3.03	7.19
Tripe and sugar . . .	6.42	14.50
Meal, bread, potatoes . .	6.06	17.23

Experiments on the rabbit also showed that in this animal both the weight of the liver and its percentage in glycogen are much diminished by several days' fasting, but are maintained at the maximum standard, for a time at least, by a diet consisting exclusively of the carbohydrates. The average results were as follows:

AVERAGE PRODUCTION OF GLYCOGEN IN RABBITS, IN THE FASTING CONDITION AND WHEN FED ON CARBOHYDRATES.

Diet for three days previously.	Absolute weight of liver (grammes).	Glycogen in the fresh liver (per cent.).
No food	34.02	1.35
Starch and sugar . . .	73.71	16.15

The quantity of glycogen found in the liver by Pavy is considerably greater than that obtained by subsequent observers under similar circumstances, and is attributed to his having employed an imperfect method of purification; but the principal fact of the increase of glycogen under the use of the carbohydrates has been confirmed by several other

[1] Leçons de Physiologie Expérimentale. Paris, 1855, p. 159.
[2] Revue des Sciences Medicales. Paris, 1874, tom. iii. p. 34.
[3] On the Nature and Treatment of Diabetes. London, 1862.

experimenters. Dock found, in his experiments on the rabbit,[1] that after from 3 to 5 days' fasting the glycogen in the entire liver was reduced to a very minute quantity, or more frequently was entirely absent. But if, in this condition, a solution of glucose were introduced into the stomach through a catheter, and the animal killed from 19 to 24 hours afterward, the quantity of glycogen contained in the liver amounted to from 0.650 to 1.243 grammes. After even 7 days' fasting, followed by an injection of glucose into the stomach, so short a time as four hours was sufficient to produce an abundance of glycogen in the liver. The deposit of this substance accordingly takes place so rapidly after the ingestion of this kind of food, that no doubt can remain of its being directly produced from the materials of the saccharine or starchy substances.

Tscherinow showed, by his observations on fowls,[2] both the production of glycogen from animal food, and also its more abundant deposit under a vegetable diet. He found that, in this species, two days' fasting was sufficient to reduce the quantity of glycogen to a minimum. After being subjected to a preliminary fast of this duration, the fowls were fed for two or three days with different kinds of food, and then killed and examined. The average results were as follows:

PRODUCTION OF GLYCOGEN IN FOWLS UNDER DIFFERENT KINDS OF DIET.

Diet previous to the experiment.	Glycogen in the fresh liver, per cent.
Fasting, 2 days	0.57
Lean meat, 2 to 4 days	1.40
Barley, 2 days	5.41
Rice, 2 days	7.21
Fibrine and sugar, 2 to 3 days	10.20

It appears furthermore from the experiments of Weiss and Luchsinger[3] that a similar increase of glycogen will take place in the liver after the ingestion of *glycerine* ($C_3H_8O_3$), a substance closely related in chemical composition to the carbohydrates, but not under the use of fat or of the alkaline tartrates or lactates.

There is accordingly every reason for the belief that the carbohydrates, when taken in with the food, are at once transported to the liver by the portal circulation, and there fixed in its substance under the form of glycogen. It makes no difference, in this respect, whether these substances be taken as starch or as sugar; since starchy matters are always transformed into glucose by the process of digestion, to be afterward absorbed by the bloodvessels of the intestine. It is under the form of glucose, therefore, that they all enter the portal circulation and thus reach the tissue of the liver. The process of the conversion of this sub-

[1] Archiv für die Gesammte Physiologie. Bonn, 1872, Band v. 571.
[2] Archiv für Pathologische Anatomie und Physiologie, 1869, Band xlvii. p. 102.
[3] Archiv für die Gesammte Physiologie, 1873, Band viii. p. 290.

stance into glycogen is a *dehydration;* that is, the separation from it of the elements of water, as follows:

$$\begin{array}{ccccc} \text{Glucose.} & & \text{Water.} & & \text{Glycogen.} \\ C_6H_{12}O_6 & - & H_2O & = & C_6H_{10}O_5. \end{array}$$

It is not possible to say in what manner or by what influence this change takes place; but it is one of the simplest actions manifested by organic substances, and is known to occur, as well as the opposite change of hydration, in many of the phenomena of both animal and vegetable nutrition. The formation of glycogen from albuminous materials is a more complicated process, and is necessarily accompanied by the appearance of another secondary product containing nitrogen; but we have no certain knowledge as to what this substance may be, or whether there may not be several new compounds formed at the same time.

Transformation of Glycogen into Sugar.—One of the most marked characters of glycogen, as extracted from the liver tissue, is its ready convertibility into glucose by contact with certain organic matters contained in the secretions and in the blood. This change takes place partially in the liver itself; and the consequence is that in a state of health the tissue of the organ always contains glucose as well as glycogen. In fact, the existence and production of sugar in the liver was a discovery anterior to that of glycogen, having been demonstrated by Bernard[1] in 1848. The experiments of this observer, the most important of which have been repeatedly confirmed by others, show that the glucose found in the liver of both carnivorous and herbivorous animals has an internal origin, and that it first makes its appearance in the hepatic tissue itself.

If a dog, cat, or other carnivorous animal, be fed for several days exclusively upon meat and then killed, the liver alone of all the internal organs is found to contain glucose. For this purpose, a portion of the organ should be cut into small pieces, reduced to a pulp by grinding in a mortar with a little water, and the mixture coagulated by boiling with an excess of sodium sulphate. The filtered fluid will then reduce the oxide of copper, with great readiness, on the application of Trommer's test. A decoction of the same tissue, mixed with a little yeast, will also give rise to fermentation, producing alcohol and carbonic acid, as is usual with saccharine solutions. On the contrary, the tissues of the spleen, the kidneys, the lungs, and the muscles, treated in the same way, give no indication of sugar, and do not reduce the salts of copper. Every other organ in the body, as well as the blood of the portal vein by which the liver is supplied, may be destitute of sugar, while the liver always contains it, provided the animal be healthy.

The presence of sugar in the liver is common to all species of animals, so far as yet known. Bernard found it invariably in monkeys, dogs, cats, rabbits, the horse, the ox, the goat, the sheep, in birds, in reptiles,

[1] Comptes Rendus de l'Académie des Sciences. Paris, 1850, tome xxxi. p. 571.

and in most kinds of fish. It was only in two species of fish, namely, the eel and the ray (*Muræna anguilla* and *Raia batis*), that he sometimes failed to discover it; but the failure in these instances was apparently owing to the commencing putrescence of the tissue, by which the sugar had probably been destroyed. In the fresh liver of the human subject, examined after death from accidental violence, sugar was found to be present in the proportion of 1.10 to 2.14 per cent. of the entire weight of the organ.

The following list shows the average percentage of sugar present in the healthy liver of man and different species of animals, according to the examinations of Bernard:

PERCENTAGE OF GLUCOSE IN THE LIVER.

In man	1.68	In ox	2.30
" monkey	2.15	" horse	4.08
" dog	1.69	" goat	3.89
" cat	1.94	" birds	1.49
" rabbit	1.94	" reptiles	1.04
" sheep	2.00	" fish	1.45

The glucose thus found in the liver originates by transformation of the glycogen of the hepatic tissue. As glycogen diminishes in quantity or disappears altogether by continued fasting, and is again produced from the ingestion of animal food, the glucose which is derived from it exhibits similar fluctuations. In the carnivorous animals, sugar is present in the liver, although no carbohydrates have been given with the food for an indefinite time. Bernard kept a dog under observation for three months upon an exclusive diet of boiled calves' heads, and another for eight months upon scalded tripe. At the end of that time the liver in each case contained the usual quantity of glucose. We have also found that in the dog, after an exclusive diet for eight days of the fresh meat of the bullock's heart, the liver contains both glycogen and sugar, while neither of these substances exists in the blood of the portal vein. The diminution of glucose by fasting, and its reappearance under the influence of animal food, were shown by Bernard in the following way: Nine rats, taken in the sewers beneath the College of France, were used for experiment. Three of them were at once killed and their livers found to be highly saccharine. The remainder were then kept without food for four days. At the end of that time three of them were killed, and their livers, upon examination, found to be nearly destitute of sugar, only slight traces being discovered, too small for quantitative determination. The glucose which existed, accordingly, in the livers of these animals at the time of their capture, had disappeared during their four days' period of fast. The remaining three were then supplied with a meal of raw beef, and when killed, six hours afterward, their livers contained an abundance of sugar.

The most distinct proof that the saccharine matter of the liver origi-

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nates in the tissue of the organ itself, by transformation of the glycogen, is that it continues to be formed for a certain length of time after death, provided the liver contain glycogen. This fact also was first shown by Bernard,[1] and is easily verified. If the liver of a healthy dog be taken out of the body immediately after death, and injected with water by the portal vein, the watery injection which escapes by the hepatic vein, after traversing the liver-tissue, will be found to contain sugar. But, as the injection is continued, the quantity of glucose extracted by it from the liver grows constantly less, until, in from half an hour to an hour, it is completely exhausted, and at the end of this time neither the injected fluid nor the hepatic tissue contains any trace of glucose. If such a liver be kept in a moderately warm place for some hours it will again be found abundantly saccharine. The glucose may be again exhausted by a fresh injection and again reproduced, until all the glycogen has been transformed or until the changes of decomposition begin to be established. The glycogen itself, being less soluble than the sugar, remains behind after such an injection, and produces a new supply of glucose by a new transformation.

Immediately after death, accordingly, if the liver be allowed to remain saturated with its natural organic juices, the transformation of its glycogen takes place at first with considerable rapidity; approximating, no doubt, the rate at which this transformation takes place during life. Within the first hour, according to our own observations in the dog, the glucose in the liver tissue is increased to between 4.81 and 5.66 times its original amount. After this the change goes on more slowly, its rate diminishing with the lapse of time, so that at the end of twelve hours the sugar may have increased to not more than 5.73 times its former quantity. The following table gives the results of three experiments in this direction.

PROPORTION OF GLUCOSE IN THE LIVER OF THE DOG, AT DIFFERENT PERIODS AFTER DEATH.

	At the end of	Per thousand parts.
No. 1.	5 seconds	810
	15 minutes	792
	1 hour	10.260
No. 2.	5 seconds	3.850
	6 hours	11.458
No. 3.	4 seconds	2.675
	1 hour	11.888
	4 hours	13.361
	12 hours	15.351

In the tables of Bernard (page 234), the results are drawn mostly from livers examined some time after death, and accordingly represent, not

[1] Gazette Hebdomadaire. Paris, 5 Octobre, 1855.

only the glucose present in the organ at the moment of death, but also that which accumulates afterward. The proportion found in the dog at the end of twelve hours corresponds very closely in both tables.

It has been doubted by some observers (Pavy, Meissner, Ritter, Schiff), whether glucose be really produced in the liver during life; its presence in the liver tissue, in ordinary examinations, being attributed entirely to a post-mortem production by transformation of the glycogen. It is true, as these experimenters have found, that if a small portion of the liver substance be cut out from the body of the living animal and instantly plunged into a freezing mixture, boiling water, or strong alcohol, so as to arrest the transformation of the glycogen, its subsequent examination may not show the presence of glucose by Trommer's test, as applied in the usual way. Professor Flint, Jr.,[1] by operating in this way with boiling water, found in two instances, where the time employed in the extraction and coagulation of the liver substance was respectively 28 seconds and 22 seconds, there was no marked or certain evidence of sugar. In another instance, where the time employed was only 10 seconds, the liver extract presented no trace of sugar whatever; and yet the blood of the hepatic vein, obtained within a minute after the first operation, showed a well-marked saccharine reaction by the copper test. We have also found, that under similar conditions, the liver tissue may yield no reduction by the copper test at the end of 17 or of 22 seconds, though it is distinct in 50 seconds after its extraction from the living body. Harley,[2] by killing the animal by section of the medulla oblongata, immediately placing a portion of the liver in a freezing mixture and afterward slicing it directly into boiling acidulated water, has shown that glucose may be demonstrated to exist in the organ within 20 seconds after the death of the animal.

But the failure to demonstrate the presence of glucose, even within the shortest time after the extraction of the liver, is only owing to the use of too small a quantity of the liver tissue and an imperfect purification of its watery extract. If these sources of error be avoided, glucose will always be found in the liver at the instant of its extraction, or as soon afterward as the necessary test can be applied. In order to demonstrate this, a portion of the liver is to be taken out of the abdomen of the living animal by an instantaneous incision, reduced to a pulpy mass by passing it between two fluted rollers, and at once dropped into a vessel of boiling water or of strong alcohol. By this means all further change of the glycogen is arrested, and the time which elapses between the extraction of the liver substance and its immersion in the coagulating liquid may be reduced to a very few seconds. A watery extract is finally to be made of the liver substance, which must be completely purified by the repeated use of animal charcoal until it is absolutely transparent

[1] New York Medical Journal, January, 1869.

[2] Proceedings of the Royal Society of London, vol. x. p. 289.

and colorless [1] after which it is tested for glucose by the use of Fehling's solution.

We have experimented, in the manner above described, upon twenty dogs. In four of the cases, the method employed was that by boiling water; in the remaining sixteen cases, that by alcohol. The animals were examined four, eight, twelve, and twenty-four hours after feeding; the food consisting always of the fresh or cooked meat of the bullock's heart. The longest time which elapsed from the separation of the liver to its immersion in alcohol or boiling water was thirteen seconds; the shortest time was three seconds. The average time was six and a quarter seconds. In every instance the final watery solution gave a distinct and perfectly unmistakable sugar reaction by the copper test. In one-half the cases, the presence of sugar alone was determined by this method; in the remainder, its proportion to one thousand parts of the liver tissue was also ascertained.

The following is a list of these experiments, with their results:

GLUCOSE FOUND IN THE LIVER OF THE DOG IMMEDIATELY AFTER ITS EXTRACTION.

Experiment.	Time after feeding.	Time consumed in taking out liver.	Process of treatment.	Proportion of glucose per thousand parts.
No. 1	4 hours	13 seconds	Alcohol	Glucose
No. 2	4 hours	7 seconds	"	"
No. 3	4 hours	10 seconds	"	"
No. 4	4 hours	4 seconds	"	"
No. 5	8 hours	7 seconds	"	"
No. 6	8 hours	6 seconds	"	"
No. 7	4 hours	5 seconds	Boiling Water	"
No. 8	12 hours	6 seconds	" "	"
No. 9	12 hours	8 seconds	" "	"
No. 10	12 hours	5 seconds	" "	"
No. 11	4 hours	9 seconds	Alcohol	2.093
No. 12	4 hours	5 seconds	"	0.804
No. 13	8 hours	7 seconds	"	1.750
No. 14	8 hours	3 seconds	"	1.510
No. 15	12 hours	5 seconds	"	1.810
No. 16	12 hours	5 seconds	"	4.175
No. 17	12 hours	7 seconds	"	1.830
No. 18	12 hours	3 seconds	"	4.375
No. 19	24 hours	5 seconds	"	3.850
No. 20	24 hours	4 seconds	"	2.675

It appears from these results, that when the requisite precautions are adopted, glucose is found in the liver at the earliest period at which it is possible to examine the organ after its separation from the body of the living animal; the average quantity of sugar existing in the liver tissue, at this time, being at least two and a half parts per thousand. The exact proportion of sugar thus present in the liver at the instant of death, or within a few seconds afterward, varies from 0.804 to 4.375

[1] All the necessary details of this process are given in the New York Medical Journal for July, 1871.

parts per thousand. These variations appear to depend upon individual differences in the animals employed for experiment; in the same manner as other ingredients of the tissues and fluids are found to vary, within physiological limits, in different individuals.

As sugar is found, under some circumstances, in minute quantity in the blood of the general circulation, there might be room for doubt whether the glucose, present in the liver at the moment of death, be not due to the arterial blood with which the organ is supplied, rather than an ingredient of the hepatic tissue. This, however, is not the case, as is shown by examining, at the same time with the liver or immediately afterward, some other abdominal organ equally well supplied with arterial blood. In the experiments above described, the spleen in three cases was taken out within ten minutes after the excision of the liver, treated in the same manner by the alcohol process, and examined for glucose with the following result:

PROPORTION OF GLUCOSE PER THOUSAND PARTS.

	At the end of	In the	
Exp. No. 14.	3 seconds	Liver	1.510
	10 minutes	Spleen	0.
Exp. No. 19.	5 seconds	Liver	3.850
	10 minutes	Spleen	0.
Exp. No. 20.	4 seconds	Liver	2.675
	10 minutes	Spleen	0.

It is evident, accordingly, that the liver sugar does not belong to the arterial blood with which the organ is supplied, but is a normal ingredient of the hepatic tissue.

The sugar formed in the liver is similar in most of its properties to the glucose derived from other sources. Its solution readily reduces the salts of copper in Trommer's or Fehling's test, and is colored brown when boiled with a solution of caustic alkali. It rapidly enters into fermentation if mixed with yeast and kept at a temperature of from 21° to 38° (70° to 100° F.). It is distinguished from other varieties of sugar, according to Bernard,[1] by the readiness with which it becomes decomposed in the blood—since cane sugar, if injected into the circulation of a living animal, passes through the system without sensible decomposition, and is discharged unchanged with the urine; sugar of milk, and glucose prepared artificially from starch, if injected in moderate quantity, are decomposed in the blood, but if introduced in greater abundance, make their appearance also in the urine; while a solution of liver-sugar, though injected in much larger quantity than either of the others, may disappear altogether in the circulation, without passing off by the kidneys.

Absorption and final Disappearance of the Liver-sugar.—The glucose produced in the liver by transformation of the glycogen does not

[1] Leçons de Physiologie Expérimentale. Paris, 1855, p. 213.

remain at the place of its formation. It is constantly absorbed by the blood traversing the capillaries of the organ, and carried away in the current of the circulation. This is shown by the fact that not only the liver tissue, but also the blood of the hepatic vein contains glucose in appreciable quantity, although it may not exist in the portal blood by which the organ is supplied. As the blood accordingly, before its entrance into the liver, in these cases, is destitute of sugar, and yet contains this substance after its passage through the organ, it must acquire its saccharine ingredients by the absorption of glucose in the liver itself. Bernard has shown[1] that if two specimens, of portal and hepatic blood, be taken from the same dog, when in a fasting condition or after an exclusive diet of animal food, the former will show no trace of sugar, while the latter will be distinctly saccharine. Lehmann[2] has obtained similar results by experimenting upon both dogs and horses. In these animals, nourished with vegetable matters, glucose was found in the blood of the portal vein, though often in very small quantities. In dogs, when under a diet of animal food, the portal blood contained no glucose, while this substance was present in the blood of the hepatic vein. The following table gives the results of Lehmann's experiments:

Quantity of Glucose in the Blood of the Hepatic Vein. as compared with that of the Portal Vein.

Species of animal.	Regimen previous to the experiment.	Proportion of glucose per thousand parts in the blood of the	
		Portal vein.	Hepatic vein.
Dog	Fasting for two days	0	7.640
"	" " "	0	6.380
"	" " "	0	8.040
"	Meat	0	8.140
"	"	0	7.990
"	"	0	9.460
"	Boiled potatoes	Traces	9.810
"	" "	"	8.540
Horse	Bran, hay, and straw	0.550	8.950
"	" " "	0.052	6.350

Glucose, accordingly, although constantly produced in the liver, does not accumulate in the organ during life, owing to its being absorbed by the blood, and carried away nearly as rapidly as it is formed. It is only after death, when the circulation has come to an end and the transformation of glycogen still goes on for a time, that the proportion of glucose in the liver tissue becomes notably increased. The circulation of blood through the organ, so long as it continues, acts like an artificial watery injection of the hepatic vessels, and extracts from its substance the sugar which has been produced at the expense of the glycogen.

[1] Leçons de Physiologie Expérimentale. Paris, 1855, p. 265, 469.

[2] Comptes Rendus de l'Académie des Sciences. Paris, 1855. Tome xl. p. 585.

Unless, therefore, a new supply of food be taken, all the glycogen of the liver, as shown by experiments cited above, becomes after a time exhausted ; having gradually undergone the saccharine transformation and absorption by the bloodvessels.

Owing to these processes going on in the hepatic tissue, the blood beyond the liver, that is, the blood in the hepatic vein, the inferior vena cava above the diaphragm, and the right side of the heart, contains traces of glucose. The proportion of sugar in the blood, however, constantly diminishes as it recedes from the point of its origin, since the saccharine blood coming from the liver is diluted with that of the inferior vena cava, and this mixture again with that of the superior vena cava, before reaching the right cavities of the heart. Beyond the pulmonary circulation, under ordinary circumstances, it has disappeared altogether, so that no sugar is to be found, as a rule, in the blood of the general circulation.

The changes, therefore, which take place in the liver, so far as regards the carbohydrates, consist, first, in a deposit of glycogen, derived from the ingredients of the blood. This glycogen acts as a reserve material, which is afterward used for the purposes of nutrition. The vegetable starch and sugar of the food, after digestion, are absorbed under the form of glucose and taken up by the vessels of the portal system. This glucose does not at once enter the general circulation, but on reaching the liver undergoes, for the most part, a conversion and deposit as glycogen, or animal starch. It then gradually again passes into the form of glucose by a secondary transformation, and in this form is carried away by the hepatic blood, to be finally decomposed or assimilated in some unknown manner for the maintenance of the vital phenomena. The final product of its metamorphosis or destruction in the animal body is undoubtedly carbonic acid and the elements of water; but how far this is accomplished by direct oxidation, or what other intermediate changes may occur in the act of nutrition, cannot as yet be determined with certainty.

Similar successive transformations of the starchy and saccharine carbohydrates are already known to take place in vegetables. In the growing plant, under various conditions, the starch, first formed in the green leaves, passes into the condition of a saccharine fluid to be transported into organs of reserve, such as tuberous roots, grains, and fruits, where it is again deposited as starch; and from these it is subsequently taken up at the requisite time as glucose, and carried by the vascular channels into the growing organs for its final destruction or assimilation.[1] Starch and sugar, therefore, in animals as well as in vegetables, are to be regarded as two different forms of the same nutritive substance, one of which is in the condition of temporary deposit, the other in that of solution and activity.

[1] Mayer, Lehrbuch der Agrikultur Chemie. Heidelberg, 1871, Band i. pp. 76, 78, 81.

Accumulation of Glucose in the Blood, and its discharge by the Urine.—The sugar formed from the glycogen of the liver, and discharged little by little into the circulation, is not usually recognizable at a distance from the organ, owing to the changes which it undergoes in the blood. But under certain conditions its quantity, or the rapidity of its discharge by the liver, may be increased; so that, its decomposition no longer keeping pace with its production, it is diffused to a greater distance from the point of its origin. Bernard has observed this to take place, in an appreciable degree, during ordinary digestion. In this process, the circulation through the liver being increased in intensity, after a time the glucose derived from its substance may become perceptible in small quantity beyond the lungs, and traces of it may appear in the arterial blood. At the same time its alteration continues to be effected, so that the venous blood, after passing through the capillaries of the general system, is no longer saccharine. This condition lasts but for a short time. As the digestive process comes to an end, and the hepatic circulation returns to its ordinary standard of activity, the glucose which it supplies to the blood is again reduced to such a proportion, that it disappears altogether from the vascular system beyond the right side of the heart.

If, however, from any cause, the quantity of glucose in the blood of the general circulation be increased beyond a certain proportion, it then fails to be completely decomposed or assimilated, and a part of it is discharged by the kidneys. Under these circumstances the urine becomes saccharine, and the animal is placed in a condition of diabetes. The proportion of glucose which the blood must contain, in order that it may be discharged by the kidneys, has been determined in several instances. Von Becker found[1] that in rabbits, if glucose be present in the blood in the proportion of 5 parts per thousand, it passes off by the urine, where it may be distinctly recognized by the copper test; but if less abundant than this, the indications of its presence in the urine are faint and uncertain. Bernard ascertained,[2] by injecting in the same animal a solution of glucose into the veins, that in general a condition of diabetes was produced when glucose was injected in larger quantity than one part per thousand of the entire bodily weight. The appearance of glucose in the urine is therefore dependent upon the proportion in which it exists in the blood. If its quantity be below a certain point, it is all decomposed by contact with the ingredients of the blood; if it be above this point, some of it escapes this change and is then eliminated as an ingredient of the urine. According to the experiments of Von Becker, a solution of glucose, injected into the jugular vein of the rabbit in sufficient quantity, may cause the appearance of sugar in the urine in less than three hours; but at the end of from six to seven hours the whole

[1] Zeitschrift für Wissenschaftliche Zoologie, Band v. p. 176.

[2] Leçons sur les Liquides de l'Organisme. Paris, 1859, tome ii. p. 73.

of it may be eliminated, so that it is no longer to be found as an ingredient of the excretions.

There are a variety of circumstances which may so increase the proportion of glucose in the blood as to cause a saccharine condition of the urine.

I. One of these causes is *an unusually abundant and rapid absorption of sugar from the intestine.* The sugar taken in with the food, or produced in the intestine by the transformation of starch, is usually changed into glycogen by the hepatic tissue, and is afterward only slowly reconverted into glucose and discharged under this form into the blood. But where a very large quantity of sugar is suddenly absorbed by the blood-vessels of the intestine and at once carried by the portal vein to the liver, the tissue of the organ is not capable of immediately converting the whole of it into glycogen. Thus a portion of the sugar taken up in this way passes through the hepatic circulation unchanged, and, reaching the general circulation in unusual quantity, is accordingly discharged with the urine. Von Becker observed that when concentrated solutions of glucose are introduced in abundance into the intestinal canal of the rabbit, it may appear subsequently in the urine. Bernard has also found that, in the rabbit after one or two days' fasting, if sugar in large amount be injected into the stomach, the urine becomes diabetic; and that the same result may follow, if the animal, in a similar fasting condition, be made to eat a considerable quantity of carrots, which are highly saccharine. The same thing has been observed by Bernard in the human subject, in consequence of taking a large supply of sugar in solution when the stomach has been empty for several hours. This result is produced, however, only when a much greater abundance of sugar is present in the intestine than occurs in ordinary digestion, and depends upon the excessive quantity absorbed within a given time.

II. A diabetic condition may also be induced by anything which *hastens the circulation of blood through the liver*, or increases its supply of blood. Many observers have met with this result, as produced by a variety of causes. Bernard has found that in dogs the blood of the venous system generally may present traces of glucose after the abdomen of the animal has been subjected to pressure or manipulation over the region of the liver, and after any continued struggles or convulsive muscular action, by which the abdominal organs are forcibly compressed In the same animal, according to the experiments of Harley, the injection of weak solutions of ammonia or of ether into the portal vein may be followed by a saccharine condition of the urine. This condition has also been seen in the human subject after a bruise received upon the right hypochondriac region. The resistance of an animal to the inhalation of ether and the subsequent muscular relaxation, general paralysis from a fracture of the skull with cerebral hemorrhage, and the action of *woorara*, or the South American arrow-poison, which also causes complete muscular paralysis, are all known to be sometimes followed by the ap-

pearance of sugar in the urine. Schiff[1] has even found that in various animals, by simply compressing the abdominal aorta for ten minutes, or by tying the principal bloodvessels of one limb, he has induced, for the time, a condition of diabetes. These different causes may all operate by accelerating the hepatic circulation as well as that of the abdominal organs generally.

III. A saccharine condition of the blood and urine may also be induced by *puncture of the medulla oblongata* in the floor of the fourth vertricle. This remarkable fact, which was first discovered by Bernard,[2] may be demonstrated in both carnivorous and herbivorous animals. It is best shown in the rabbit by introducing a narrow chisel-shaped instrument, with the cutting edge directed transversely, through the back part of the skull and the cerebellum, so that it shall pierce the posterior part of the medulla exactly in the median line, without passing completely through its substance. Glucose appears in the urine after from one to two hours and continues to be present for two or three days. The immediate effect of this operation, according to the direct observations of Bernard, is to increase the activity of the abdominal and hepatic circulation. It is not due to a direct influence conveyed by the pneumogastric nerve, since the result follows, as usual, although the pneumogastric nerves may have been divided, and neither division nor irritation of these nerves produces a similar effect. When successfully performed, the operation causes no serious disturbance of the vital functions, and the animal recovers after a few days without suffering permanent injury.

In all the instances above mentioned, the appearance of sugar in the urine is only temporary, depending upon an occasional disturbance of the circulation. When in the human subject this condition becomes permanent, it constitutes the disease known as *Diabetes mellitus*. In this affection, which is generally progressive and fatal, the urine is increased in quantity, of greater specific gravity than natural, and continuously charged with sugar, sometimes in excessive abundance. Fluctuations are observable in the quantity of glucose discharged at different periods of the digestive process, but it may continue to appear, even when no starchy or saccharine matter is taken with the food.

[1] Journal de l'Anatomie et de la Physiologie. Paris. 1866. No. iv. p. 365.
[2] Leçons de Physiologie Expérimentale. Paris, 1855, p. 290.

CHAPTER XII.

THE BLOOD.

THE blood, in its natural condition, while circulating in the vessels, is a thick opaque fluid, varying in different parts of the body from a brilliant scarlet to a dark purple or nearly black color. It has a slightly alkaline reaction, and a specific gravity of 1055. It consists, first, of a nearly colorless, transparent, alkaline fluid, termd the *plasma*, containing water, fibrine, albumen, and salts, in a fluid condition; and, secondly, of a large number of distinct cells, or corpuscles, the *blood-globules*, swimming freely in the liquid plasma. The globules form about 40 per cent., and the plasma about 60 per cent., by volume, of the entire mass. The specific gravity of the two ingredients is somewhat different. That of the plasma is about 1030; that of the globules, 1088. Their relative quantities by weight are therefore more nearly equal to each other than when estimated by volume; the exact proportions, according to Robin, being nearly 45 per cent. of globules and 55 per cent. of plasma.

Notwithstanding the difference in specific gravity between the blood-globules and the plasma, the natural movement of the blood in the vessels keeps them thoroughly mingled; and even when the blood is allowed to remain at rest in a glass jar, the globules subside only very slowly and imperfectly. Thus the globules, disseminated uniformly throughout the plasma, give to the entire mass of the blood an opaque aspect and a deep red color.

The globules of the blood are of two kinds, namely, red and white; of these the red are by far the most numerous.

Red Globules of the Blood.

The red globules of human blood are so abundant that, in the thinnest layer under the microscope, they appear crowded together in such profusion as to cover or touch each other in every direction. According to the estimates of Welcker and Vierordt about 5 millions of them are contained in each cubic millimetre of blood. On account of their quantity therefore, as well as their peculiar properties, it is evident that they form a most important constituent of the circulating fluid.

Physical Properties of the Red Globules.—The red globules of human blood present, under the microscope, a perfectly circular outline and a smooth exterior. According to the most recent and careful measurements of various observers, they have, on the average, a transverse diameter of from 7.50 to 7.75 mmm. Their size varies more or less, but this variation is not very marked for the greater number of the

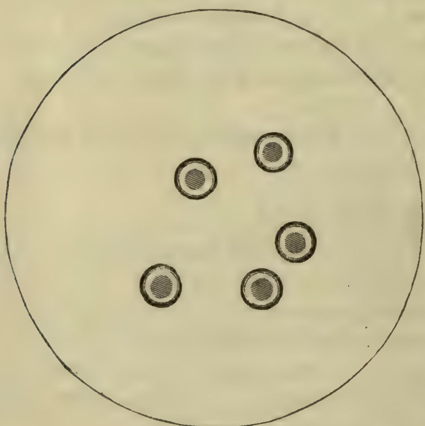
globules, and, according to the observations of Schmidt, over 90 per cent. of those contained in a single specimen have the same dimensions. The smallest size observed is 4.50 mmm. (Harting), and the largest 9.3 mmm.; while their average diameter, as found in different individuals, varies from 6.70 to 8.20 mmm.

Fig. 76.

Human Blood-globules.—*a*. Red globules, seen flatwise. *b*. Red globules, seen edgewise. *c*. White globule.

The form of the red globule is that of a spheroid, very much flattened on its opposite surfaces, somewhat like a thick piece of money with rounded edges. The globule accordingly, if seen flatwise, presents a comparatively broad surface and a circular outline (Fig. 76, *a*); but if it be made to roll over, it will present itself edgewise during its rotation, and assume the flattened form indicated at *b*. The thickness of the globule, seen in this position, is about one-fifth of its transverse diameter. When the globules are examined lying upon their broad surfaces, it can be seen that these surfaces are not exactly flat, but that there is on each side a slight central depression, so that the rounded edges of the blood-globule are evidently thicker than its middle portion. This inequality produces a remarkable optical effect. The substance of which the blood-globule is composed refracts light more strongly than the fluid plasma. Therefore, when examined with the microscope by transmitted light, the thick edges of the globules act as double convex lenses, and concentrate the light above the level of the fluid. Consequently, if the object-glass be carried upward by the adjusting screw of the microscope, and lifted away from the stage, so that the blood-globules fall beyond its focus, their edges will appear brighter. But the central portion of each globule, being excavated on both sides, acts as a double concave lens, and disperses the light from a point be-

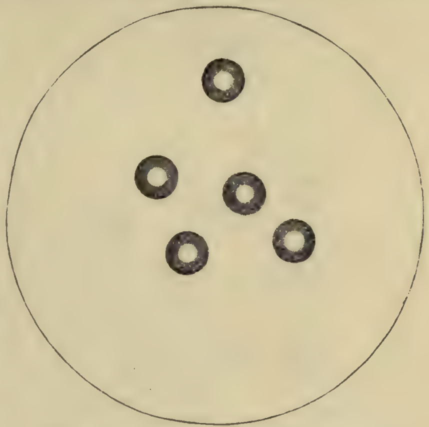
Fig. 77.



Red Globules of the Blood, seen a little beyond the focus of the microscope.

low the level of the fluid. It thus becomes brighter as the object-glass is carried downward, and the object falls within its focus. An alternating appearance of the blood-globules may, therefore, be produced by viewing them first beyond and then within the focus of the instrument. When beyond the focus, the globules will be seen with a bright rim and a dark centre (Fig. 77). When within it, they will appear with a dark rim and a bright centre. (Fig. 78.)

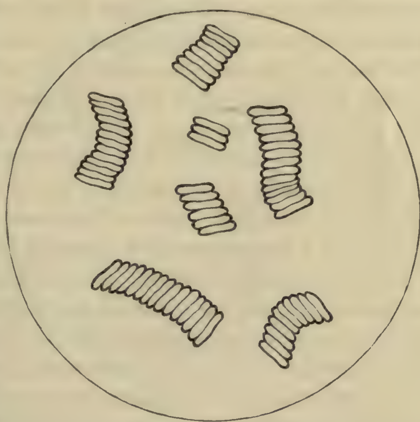
Fig. 78.



THE SAME, seen a little within the focus.

Within a minute after being placed under the microscope, the blood-globules, after a fluctuating movement of short duration, often arrange themselves in slightly curved rows or chains, in which they adhere to each other by their flat surfaces, presenting an appearance which has been aptly compared with that of rolls of coin. This is probably owing to the coagulation of the blood, which takes place very rapidly when spread out in thin layers and in contact with glass surfaces; and which, by compressing the globules, forces them into such a position that they occupy the least possible space.

Fig. 79.



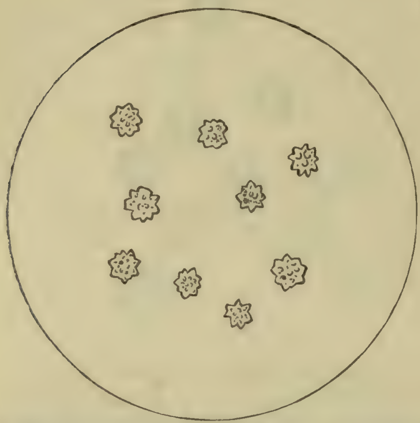
RED GLOBULES OF THE BLOOD, adhering together, like rolls of coin.

The color of the blood-globules, when viewed by transmitted light and in a thin layer, is a light amber or pale yellow. It is deep red when seen by reflected light, or in thick layers. The blood-globules have a consistency which is very nearly fluid They are exceedingly flexible, and easily elongated, bent, or distorted by pressure in passing through the narrow currents of fluid which often establish themselves in a drop of blood under microscopic examination; but regain their original shape as soon as the pressure is taken off.

So far as immediate observation can show, the red globules of the blood, in man and the mammalians, are homogeneous in structure. The most careful examination fails to show, with any certainty, the evidence

of an external envelope, distinct from the parts contained within it; and although some microscopists of high authority (Kölliker, Richardson) continue to regard the existence of such a cell-membrane as probable, it is not generally admitted, and cannot be directly demonstrated. Each globule appears to consist of a mass of organic substance, presenting the same color, consistency, and composition throughout.

Fig. 80.



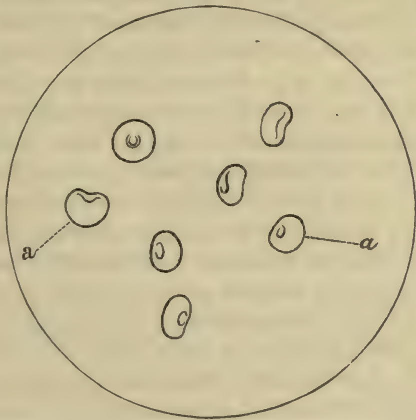
Red Globules of the Blood, shrunken, with their margins crenated.

The appearance of the blood-globules is altered by various physical and chemical reagents. If a drop of blood, when placed under the microscope, be not protected from evaporation, the globules near the edges of the preparation often diminish in size, becoming shrivelled and crenated, presenting an appearance as if minute granules were projecting from their surfaces; an effect apparently produced by the loss of a part of their watery ingredients. This distortion of the globules sometimes takes place with great rapidity, and care is requisite not to confound a change produced by external physical causes with morbid alteration of the ingredients of the blood. According to the observations of Kölliker, this, as well as certain other abnormal forms presented by the blood-globules, is never to be seen in the blood while circulating in the vessels.

If water, on the other hand, be added to the blood, so as to dilute the plasma, the red globules absorb it by imbibition, lose the central concavity of their flat surfaces, assume the spherical form, and become paler. If a larger quantity of water be added, it may dissolve out completely the coloring matter, leaving the globules as pale, colorless circles, which are almost invisible on account of their tenuity. They may still, however, be brought into view by the addition of an iodine solution, which stains them of a yellowish color. If the water added to the blood be moderate in quantity, just sufficient to be taken up by imbibition by the globules, but not to extract their coloring matter, a special change in their form is exhibited. The edges of the globules, being thicker than the central portions, and absorbing water more abundantly, become turgid, and encroach gradually upon the central part. (Fig. 81.) It is very common to see the central depression, under these circumstances, disappear on one side before it is lost on the other, so that the globule, as it swells up, curls over toward one side, and assumes a peculiar cup-shaped form. (Fig. 81, *a*, *a*.) This figure may often be seen in blood-globules after soaking for some time in the urine,

or other animal fluids of less density than the plasma of the blood. Dilute acetic acid, added to the blood, instantly extracts the coloring matter of the red globules, reducing them to the condition of pale and nearly invisible colorless bodies. After the action of water, however, these colorless cells remain for a long time, and are dissolved very slowly in comparison with the coloring matter.

Fig. 81.



RED GLOBULES OF THE BLOOD, after the imbibition of water.

Dilute alkaline solutions, on the contrary, dissolve readily the whole substance of the blood-globules. A solution of potassium hydrate, in the proportion of ten per cent., acts most rapidly in this manner. Solutions of soda and ammonia have a similar effect, although less promptly than the preceding.

Solutions of sodium glycocholate or taurocholate, in any grade of concentration, or of the fresh bile itself, as shown by Kühne, have also the property of dissolving completely the red globules of the blood.

Composition of the Red Globules.—The red globules are composed of an albuminous and a coloring matter, together with mineral salts and a certain proportion of water. According to Lehmann, the water of the red globules amounts to 688 per thousand parts, and a little over 8 parts per thousand consist of mineral salts, namely, sodium and potassium chlorides, phosphates, and sulphates, together with lime and magnesium phosphates.

By far the most important ingredient of the red globules is undoubtedly their coloring matter, or *hemoglobine*, the main characters of which have been described in Chapter V. According to the estimates of Preyer,[1] founded upon the observed quantity of iron as an ingredient, the average proportion of hemoglobine in healthy human blood is 12.34 per cent. As the globules themselves constitute 45 per cent of the whole blood, the quantity of hemoglobine in each blood globule is about 27 per cent. of its entire mass, or 86 per cent. of its solid ingredients. It is, accordingly, as regards its quantity, the principal substance of which the globules are composed.

In the fresh globule, the hemoglobine is united with another substance which is colorless and undoubtedly albuminous in its nature, and which forms a substratum for the other ingredients of the globules. This colorless matter is less soluble in water than the hemoglobine, and it is

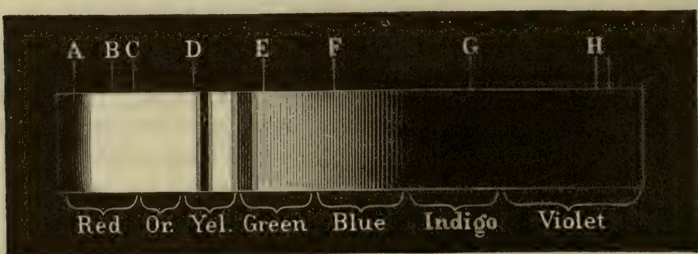
[1] Die Blutkrystalle, Jena, 1871, p. 117.

owing to this fact, already mentioned, that when water is added to the blood in sufficient quantity, the hemoglobine may be entirely extracted from the globules in a state of solution, leaving behind the colorless substratum, much reduced in volume, but still remaining undissolved for a considerable time. The exact physical condition of the hemoglobine in the blood-globule and its mode of union with the colorless substratum are not positively known. Preyer calculates that the water of the blood-globule is quite insufficient in quantity to hold in solution, by itself, the hemoglobine which is present; and, according to the same observer, it cannot exist in the blood-globules in a solid form, since the crystals of hemoglobine are always doubly refracting, while the fresh globules themselves are never so. So far as we can judge, the two substances are united uniformly throughout the mass, in a condition of thick or tenacious semi-fluidity; but the hemoglobine is more easily affected by various artificial dissolving agents, and by this means may be extracted from the mass of the globule.

Hemoglobine is remarkable for the avidity with which it absorbs oxygen whenever, either as constituent of the blood-globules or in the form of solution, it is brought in contact with this gas or with atmospheric air. The brilliant red color presented by its solutions depends upon the quantity of oxygen present; for if this substance be exhausted by means of the air-pump, the application of heat, or the displacing action of an indifferent gas, the clear scarlet hue of the solution disappears and is replaced by a dull red or purple color.

Solutions of pure hemoglobine, as well as the blood-globules themselves, or diluted mixtures of blood and water, in the aerated condition, exhibit a well-marked and peculiar *spectrum.* This spectrum is distinguished by the existence of two absorption bands between the lines D and E, and situated, the one in the yellow, the other at the commencement of the green. The first of these absorption bands is comparatively

Fig. 82.



Spectrum of Hemoglobine, in Aerated Blood.

narrow, well defined, and dark, and is placed at about one-fifth the distance from D to E. The second is double the width of the first, but is less dark, and not so well defined; it occupies nearly the last half of the space between D and E. Beyond the second band the light of the

spectrum gradually diminishes, and ceases altogether about the termination of the blue, midway between F and G.

If the solution or mixture be much concentrated, or be viewed in a very deep layer, it is too opaque for spectroscopic examination, and may shut off all the light of the spectrum except a little of the red and orange; if it be too dilute, it will fail to exhibit the distinguishing characters of hemoglobine. A solution of a certain grade of strength, which allows an abundance of light to pass through, and is yet sufficient to cause its marked absorption at particular points of the spectrum, is to be used for examination. With pure hemoglobine, according to Preyer, a solution of about 1.5 parts per thousand gives the most marked results. With fresh blood, if one volume of the defibrinated blood be diluted with one hundred volumes of water, and the mixture viewed in a layer of one centimetre, all the characteristic traits of the spectrum will be distinctly shown.

The spectroscopic characters above described form a very delicate test for the coloring matter of blood. According to Preyer, with a solution of pure hemoglobine in water, of 4 parts per ten thousand, the absorption bands may still be seen, though the second one is very faint. Fresh dog's blood, if diluted with 1000 parts of water and viewed in a layer of 3 centimetres' thickness, will show a spectrum in which both absorption bands are distinctly perceptible though not very strong. If diluted with 10,000 parts of water and viewed in a layer of 4.5 centimetres, the first band is still visible, though very faint; the second is entirely imperceptible.

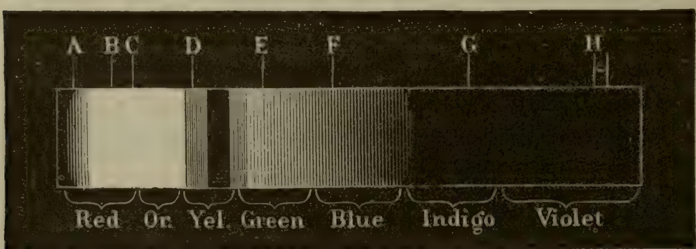
These characters are also of value in showing that hemoglobine, as extracted in the crystalline form, is identical with the normal coloring matter of the fresh globules. A solution of crystallized hemoglobine gives the same spectrum with solutions of fresh blood or with the dried globules. Even the blood while still circulating in the vessels may be made to exhibit the same appearances. If a spectroscope eye-piece with two prisms be attached to the body of a microscope in such a way that two spectra may be seen in the field, one above another, one of them formed by the light coming through the body of the instrument, the other by that coming through a lateral opening in the eye-piece; and if the mesentery of a living frog be placed before the objective of the microscope, while a solution of human blood is placed at the lateral opening, it will be seen that the absorption bands in the two spectra are the same, and exactly correspond with each other.

In all the above cases the blood which yields the characteristic spectrum already described is in the aerated condition. Even if venous blood be taken for examination, the process of extracting it and placing it in a suitable vessel for examination brings it in contact with the atmosphere and thus restores it to the condition of arterial blood. In the mesentery of the living frog, when extracted from the abdomen and spread out under the microscope, the free access of air to the peritoneal surface constantly supplies the circulating blood with oxygen; and accordingly

no marked difference, either of color or of spectroscopic characters, is to be seen between the blood in the arteries and capillaries, and that in the veins. But if by any means the blood or a solution of hemoglobine be deprived of its oxygen, and examined in that condition, it at once shows a decided change both in color and spectroscopic appearances.

This reduction or deoxidation of the coloring matter of the blood may be effected in either of two ways, namely, first, by the addition of deoxidizing agents, and secondly by keeping the blood for a time excluded from the access of air. According to the experiments of Stokes, the addition of iron protosulphate to fresh blood reduces the hemoglobine, and changes its color from bright red to dark purple; the scarlet color being again restored by agitating the blood with oxygen or atmospheric air. Other observers have accomplished the reduction of the hemoglobine by continued treatment of the blood or its solutions with a stream of carbonic acid. The second method, however, is more easily applied. If a solution of fresh blood, of a bright scarlet color, which yields a spectrum with the absorption bands of aerated hemoglobine fully developed, be inclosed in a securely stoppered test-tube, the whole of which it completely fills, and be kept in this condition secluded from the air for twenty-four or forty-eight hours, the hemoglobine at the end of that time will have lost its oxygen which has entered into other combinations. If now placed before the spectroscope, the solution will show a spectrum in which the two absorption bands above described have disappeared, and which shows in place of them a single wide and comparatively ill-defined band covering about three-quarters of the distance from D to E, and extending usually toward the red a little beyond the situation of the line D. The darkest part of this absorption band occupies exactly the space which intervened between the two former bands.

Fig. 83.



Spectrum of Reduced Hemoglobine.

If the solution be now shaken up for a few instants with atmospheric air, its bright color is at once restored, and at the same time the single absorption band of reduced hemoglobine disappears, and is replaced by the two normal bands of oxidized or aerated blood. These changes may be repeated until the blood begins to show the effect of putrefaction.

Red Globules of the Blood in different Classes of Animals.—In all vertebrate animals the blood contains red globules, of which the color-

ing matter is identical with that in the human species. Even in *Amphioxus*, a kind of fish of very low grade of organization, which was long regarded as exceptional in this respect, the existence of faintly colored globules has been demonstrated of late years. That the coloring matter of these globules consists of hemoglobine has been demonstrated in such different animals as the dog, fox, cat, horse, sheep, pig, lion, cougar, baboon, bat, hedge-hog, rat, guinea-pig, squirrel, mole, goose, pigeon, lark, owl, crow, lizard, python, tortoise, frog, carp, perch, herring, and pike. It has been discovered, in all, in 22 species of mammalians, 7 birds, 5 reptiles, and 12 fish; and has been found to exist in every species of vertebrate animal which has been examined for that purpose. Even in several invertebrate species where the blood is of a red color, although it exhibits no distinct globules, it has been found to contain hemoglobine in a state of solution. Preyer found that the red circulating fluid of the earthworm, when examined by the spectroscope, yielded a spectrum with two absorption bands identical with those of human hemoglobine. It has also been discovered in the blood of the pond-snail, the horse-leech, and the fresh-water shrimp.

But although in all these cases the red globules contain the same coloring matter, they present, in different animals, variations of form, size, and structure, which are more or less characteristic of the different classes, families, and species, to which they belong.

In the *mammalians*, or warm-blooded quadrupeds, the red globules of the blood have without exception the same homogeneous structure as in man. They have also invariably the same disk-like figure, with a circular outline, except in the species belonging to the family of the camelidæ (camel, dromedary, lama), where the disks have an oval form. The size of the red globules in the mammalians varies much in extreme cases; the smallest known being those of the Java musk-deer, an animal not larger than a rabbit, which have a diameter of 2.50 mmm., while the largest are those of the elephant, which measure 9.20 mmm. The relative size of the globules, however, in different species, does not constantly correspond with that of the animal itself; since those of the cat are larger than those of the sheep, and those of the rabbit larger than either. The following list gives the size of the red globules in various species of mammalians, according to the measurements of Gulliver and Welcker:

Diameter of the Circular Red Globules of Mammalians, in micro-millimetres.

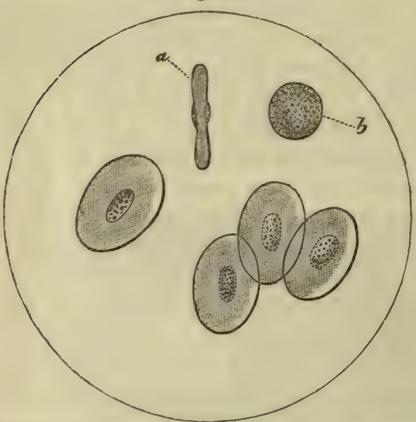
Ape	7.35	Horse	5.43
Dog	7.30	Sheep	5.00
Wolf	6.94	Red deer	5.00
Rabbit	6.90	Goat	4.10
Cat	6.50	Elephant	9.20
Fox	6.10	Two-toed sloth	8.93
Ox	5.95	Java musk deer	2.50

In animals where the red globules are of comparatively smaller size they are proportionally more numerous. It is estimated by Kölliker that the entire volume or mass of all the red globules together, in any determinate quantity of blood, does not vary much in different species; and that accordingly, in blood containing the smaller and more abundant globules, the extent of their surface, and probably their functional activity, is greater than where they are larger and less numerous. This will apply also to the inferior groups of vertebrate animals, in which the globules are often very much larger and at the same time less abundant than in man.

In the *birds*, *reptiles*, *and fish*, comprising all the oviparous vertebrata, as well as some which are viviparous, the red globules are distinguished by two very marked characters of shape and structure; namely, an oval form and the presence of a granular, colorless nucleus. The only known exception is in two species of fish belonging to the family of the Lampreys, in which the globules have a circular outline; but here also they are provided with a nucleus, and accordingly readily distinguishable from the circular globules of mammalia.

It is among the Batrachians, or naked reptiles, that the red globules present the largest size and exhibit most distinctly their structural character. They are of a regularly oval form, their short diameter being between one-half and three-quarters the long one, a little thicker toward the edges and thinner in the middle; the round or oval nucleus projecting slightly from the lateral surface at its central portion In their reactions toward different physical and chemical agents, they resemble the red blood-globules of mammalians.

Fig. 84.



BLOOD-GLOBULES OF FROG.—*a.* Blood-globule seen edgewise. *b.* White globule.

In the frog, the red globules have a long diameter of 22 mmm., or nearly three times that of the human globules; in Proteus anguinus, the blind water-lizard of the Carniola grottoes, 58 mmm.; in Menobranchus, an allied species inhabiting the northern lakes of the United States, 62.5 mmm.; and in Amphiuma tridactylum, the great water-lizard of Louisiana, according to Dr. Riddell, the red globules are one-third larger than in Proteus, or about 77 mmm. The following list gives the size of different globules of the oval form.

LONG DIAMETER OF THE OVAL RED GLOBULES OF BIRDS, REPTILES, AND FISH, in micro-millimetres.

Pigeon	14.7	Frog	22.0
Fowl	12.1	Triton	29.3
Duck	12.9	Menobranchus	62.5
Tortoise	20.0	Carp	13.1
Lizard	16.4	Sturgeon	13.4
Alligator	19.2	Perch	12.0

Diagnosis of Blood, and the distinction between Human Blood and that of Animals.—It is often of consequence to recognize the existence of blood in various animal fluids in physiological experiments, and it sometimes becomes important in medico-legal investigations. For this purpose, in the fresh fluids, nothing can be more satisfactory than spectroscopic examination; a very small quantity of hemoglobine, as already shown, being sufficient to yield a spectrum with the characteristic absorption bands. There is a further advantage in this method, namely, that it will enable us to detect the presence of blood in fluids where the red globules have been dissolved and the coloring matter reduced to a fluid condition. The washings of a blood spot or stain may therefore show the spectrum of hemoglobine, although they may not contain any red globules perceptible by the microscope. This, however, only shows the presence of the coloring matter of blood, and thus allows us to distinguish blood from other colored fluids; it does not enable us to make a distinction between the blood of man and that of animals, since the hemoglobine is the same in all.

But by microscopic examination of the red globules, either when fresh or after having been dried and again moistened, we can often distinguish the blood of an inferior animal from that of the human subject. According to the observations of Prof. J. G. Richardson,[1] a fragment of a blood spot, weighing less than $\frac{1}{180}$ of a milligramme, which had been kept in the dried condition for five years, when decolorized with a weak watery solution (0.75 per cent.) of sodium chloride, and afterward tinted with a solution of aniline, exhibited the blood-globules in such a condition that their size could be accurately measured.

If a blood stain, accordingly, which in a watery solution gives the common spectrum of hemoglobine, be found to contain oval nucleated globules, this would show it to be the blood of a bird, reptile, or fish; and the oval form alone would show that it is not human blood. The question, therefore, whether a particular specimen be composed of human blood may often be decided with certainty *in the negative* by microscopic examination. But if the specimen contain circular globules, without nuclei, it will be impossible to say positively, in any instance, that they belong to human blood, and not to that of some animal, such as the ape or the dog, whose red globules nearly approach the human in size. In most of the domesticated quadrupeds, the globules are smaller than in

[1] Monthly Microscopical Journal. London, September 1, 1874, p. 140.

human blood; but in both the sloth and the elephant, they are larger. If it were only required to decide whether a given specimen of fresh blood belonged to man or to the musk deer, for example, or even to the goat, no doubt the difference in size of the globules would be sufficient to determine the question.

But within nearer limits of resemblance it would be doubtful, because the size of the red globules varies to some extent in each kind of blood; and in order to be certain that a particular specimen were human blood, it would be necessary to show that the smallest of its globules were larger than the largest of those belonging to the animal in question, or *vice versa.* The limits of this variation have been tolerably well defined for human blood, but not sufficiently so for many of the lower animals to make an absolute distinction possible.

In the examination of stains or blood spots, the difficulty is increased by the fact that the drying and subsequent moistening of the globules introduces another element of uncertainty as to their exact original size.

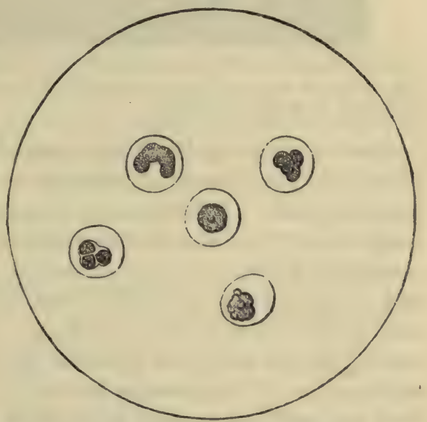
Physiological Function of the Red Globules.—There is no doubt that the red globules of blood serve mainly as the carriers of oxygen. The extreme readiness with which they absorb this substance from the atmosphere or from any other gaseous mixture containing it, their immediate change of color depending upon the supply or withdrawal of oxygen, corresponding with the change of color in the blood as it traverses the lungs or the capillaries of the general circulation, all indicate that they have a special relation to the introduction and distribution of oxygen in the living body. As a general rule, in those animals where the red globules are of large size and few in number, the activity of the vital functions is below the average; while in the species where they are smaller and more numerous, the processes of respiration, circulation, nutrition, and movement are increased in rapidity to a similar degree. The strongly marked physical and chemical characters of the red globules correspond with their importance in the functions of vitality.

White Globules of the Blood.

Beside the red globules above described, the blood contains a certain number of other cellular bodies, which differ from the former in several important particulars. These are the *white* or *colorless corpuscles.* As their name implies, they are destitute of red or other coloring matter, but under many circumstances present under the microscope a glistening appearance, and when collected in large quantity may give to the fluid or clot which contains them a whitish hue. They are much less abundant than the red globules, the average proportion in healthy human blood being one white globule to 300 red. They are nearly spherical in form, and measure, on the average, 11 mmm. in diameter. They are accordingly, in human blood, distinctly larger than the red globules. (Fig. 76, *c.*) As regards their structure, they consist of a soft, somewhat viscid, colorless, finely granular substance, containing in its interior one, two, or three ovoid nuclei. They are less yielding and

slippery than the red globules, and have a tendency to adhere more readily to the surfaces with which they are in contact; so that if a small quantity of a watery fluid be added to the drop of blood under examination, the red globules will be hurried away by the currents produced, while the white globules lag behind, and, if the irrigation be continued, may finally be left alone in the field of the microscope. Their transparency is such that, when slowly rolling over with the current, the granules in their interior may often be perceived to rotate past each other, above and below, with the motion of the globule. The nuclei are sometimes visible in the perfectly fresh globule, but may always be brought into view by the addition of pure water or of dilute acetic acid. The action of these fluids is to cause a slight swelling of the globule and to increase the transparency of its substance, by which the nuclei become perceptible as sharply defined ovoid or vesicular bodies in or near the central part of the mass. By the prolonged action of acetic acid, a portion of the cell substance becomes condensed about the nuclei in various irregular forms, while the remainder appears as a perfectly transparent and homogeneous material, surrounded by a very delicate circular outline. The final effect of both water and acetic acid is to disintegrate the white globules and cause their disappearance. Dilute alkalies dissolve them with great readiness.

Fig. 85.



WHITE GLOBULES OF THE BLOOD; altered by dilute acetic acid.

Amœboid Movements of the White Globules.—These movements are so called from their resemblance to the motions of *Amœba*, a minute gelatinous creature, of very simple organization, living in fresh-water pools and ditches. They are never to be seen while the blood is circulating in a normal manner within the bloodvessels, where the white globules always present their natural rounded form and uniformly granular appearance. But within a short time after the blood has been withdrawn from the vessels, provided it be maintained at or near the normal temperature of the animal, the white globules may be seen to alter their shape in a very remarkable way. The first indication of the change is that a certain portion of the rounded outline of the globule becomes faint and irregular, its substance at this point flattening out and extending itself into one or more transparent and homogeneous looking prolongations. These prolongations are alternately protruded and retracted, sometimes extending into long filamentous processes,

sometimes into shorter expansions with rounded ends. Variations in the form of the globule are thus produced which succeed each other with different degrees of rapidity according to circumstances. In man and the warm-blooded animals, the blood under examination requires to be kept at about the normal temperature of the body, in order that these appearances may be exhibited; but in the cold-blooded animals they may be shown at the ordinary temperature of the air.

Fig. 86.

CHANGES IN FORM OF A SINGLE WHITE GLOBULE of the blood of the Newt (*Triton millepunctatus*) occurring in an interval of seven minutes, and within half an hour after its extraction from the living body.

Besides showing these changes of form, the white globules of the blood may sometimes be seen, by a similar mechanism, to *move* from place to place. In these cases, the globule first sends out the pale prolongations of its substance as above described. The granulations of the remaining portion are then propelled, by a kind of flowing movement, into the prolongations, which thus become granular, and at the same time assume a more rounded form. The remaining portion is subsequently drawn after and into the part previously expanded; and by a continuance of this process the whole mass makes a slow progression from one point to another in the field of the microscope.

These movements are accomplished, like those of the amœba, by alternate local contractions and relaxations of the substance of the globule. In Amœba princeps the movement of progression may take place at the rate of 73 micro-millimetres per minute, and in some forms of gelatinous animalcules is occasionally so active that it may be followed continuously by the eye. But in the white globules of the blood it is much more slowly performed, and, like that of the hour hand of a clock, is to be distinguished only by noting their change of position after a certain interval of time. The white globules of the frog, when upon the free surface of the mesentery, may be seen to move at a rate, as measured by the micrometer, of 13 micro-millimetres per minute; and similar granular corpuscles, in the meshes of the connective tissue of the mesentery itself, may progress at the rate of 3.5 micro-millimetres in the same time. Certain changeable cells in the tissue of the frog's cornea, which are regarded by some observers as identical in character with the white globules of the blood, may change their position in the substance of the cornea at the rate of 2.5 micro-millimetres per minute.

The amœboid movements of the white globules of the blood are also sometimes to be seen in the interior of the capillary bloodvessels or

small veins, when imprisoned in a stagnant portion of the blood-plasma. But if the circulation be re-established, and the globules again move with the blood current, they cease to be distorted, and resume their original rounded form.

The precise physiological properties and functions of the white corpuscles cannot be determined so distinctly as in the case of the red globules. Their great inferiority in number shows that they are less important for the immediate continuance of the vital operations; and the same thing may be inferred from their want of strongly marked specific characters. For while the red globules of the blood vary in appearance to a marked degree in different classes and orders of animals, the white globules present nearly the same general features of size, form, and structure throughout the series of vertebrate animals.

Plasma of the Blood.

The plasma of the blood is the transparent, colorless, homogeneous liquid, in which the blood-globules are held in suspension. It consists of water, holding in solution various mineral salts, and of certain albuminous matters, which are distinguished by their modes of coagulation, the principal of which are known as fibrine and albumen.

Ths plasma of the blood, according to the estimates of Lehmann and Robin, has, on the average, the following constitution:

COMPOSITION OF THE BLOOD-PLASMA.

Water		902.00
Albumen		75.00
Fibrine		3.00
Fatty matters		2.50
Crystallizable nitrogenous matters		4.00
Other organic ingredients		5.00
Sodium chloride Potassium chloride Sodium carbonate Sodium and potassium sulphates Sodium and potassium phosphates Lime and magnesium phosphates	Mineral salts	8.50
		1000.00

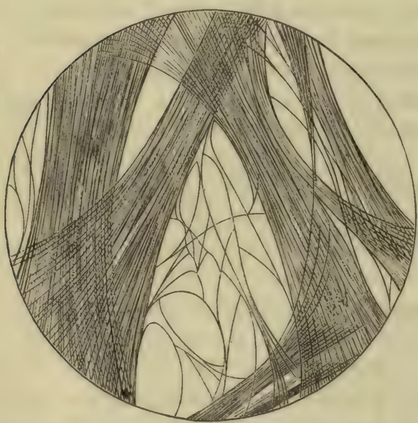
The above ingredients are all intimately mingled in the blood-plasma, in a fluid form, by mutual solution; but they may be separated from each other for examination by appropriate means. The two ingredients which on account of their nature and properties have received the greatest attention, are the fibrine and the albumen.

The *fibrine* cannot be obtained for examination under the form in which it naturally exists in the blood, since it is only to be separated from the other albuminous ingredients by undergoing the process of coagulation. Notwithstanding that this substance, or the material from which it is derived, is present in the blood in so small a quantity as three parts per thousand, it is evidently an important element in the

constitution of the circulating fluid, since it is upon its power of spontaneous solidification that the coagulability of the entire blood depends. This process takes place, under all ordinary conditions, soon after the blood has been withdrawn from the circulation; and the fibrine may be obtained in a state of tolerable purity by continuously stirring freshly-drawn blood with glass rods or a bundle of twigs. When coagulation occurs, the fibrine solidifies in the form of thin layers adherent to the surface of the rods or twigs. It at first contains, entangled with it, some of the red globules of the blood with their coloring matter; but these, as well as other foreign substances, may be removed by subjecting the mass for a few hours to the action of running water. The fibrine then presents itself under the form of nearly white threads and flakes, having a semi-solid consistency and a considerable degree of elasticity.

Coagulated fibrine, if examined in thin layers, is seen to have a fibroid or filamentous texture. The filaments of which it is composed are colorless and elastic, and when isolated are seen to be exceedingly minute, being not more than 0.5 mmm. in diameter. They are partly so placed as to lie parallel with each other, and this is probably their arrangement throughout the undisturbed fibrinous layer; but when torn up for microscopic examination, its filaments are seen to be in many spots interlaced with each other in a kind of irregular network. On the addition of dilute acetic acid the filaments become swollen, transparent, and fused into a homogeneous mass, but do not dissolve. They are often interspersed with minute granules, which render their outlines more or less obscure.

Fig. 87.



COAGULATED FIBRINE, showing its fibrillated condition.

Once coagulated, fibrine is insoluble in water and can only be again liquefied by the action of an alkaline or strongly saline solution, by prolonged boiling at a very high temperature, or by digesting with gastric juice or an acidulated solution of pepsine. These agents, however, produce a permanent alteration in the properties of the fibrine, and after being subjected to their influence it is no longer the same substance as before.

The quantity of fibrine which may be extracted from the blood varies in different parts of the body. According to most observers, venous blood in general yields less fibrine than arterial blood. A portion of it therefore disappears in passing through the capillary circulation. In

the liver and the kidneys this disappearance is so complete that no fibrine is to be obtained, as a general rule, from the blood of the renal or the hepatic veins. On this account, also, the blood in the large veins near the heart is more deficient in fibrine than in those at a distance; since the venous blood coming from the general circulation, and containing a moderate quantity of fibrine, is mingled, on approaching the heart, with that of the renal and hepatic veins, in which the coagulating material is entirely absent.

The *albumen* of the plasma is undoubtedly the most important of its ingredients in regard to the process of nutrition, since it is by far the most abundant of the albuminous matters present. It coagulates at once on being heated to 72° (162° F.), or by contact with alcohol, the mineral acids, or their metallic salts, or with potassium ferrocyanide in an acidulated solution. It exists naturally in the plasma in a fluid form by reason of its union with the water. The greater part of the water of the plasma being united with the albumen, when this latter substance coagulates, the water remains in combination with it, and assumes at the same time the solid form. If the plasma of the blood, accordingly, after removal of the fibrine, be exposed to a boiling temperature, it solidifies almost completely, so that only a few drops of water can be drained away from the coagulated mass. The earthy phosphates are also retained by the solidified albuminous mass.

The substance existing in the blood-plasma, however, and designated as albumen, appears to consist really of two different ingredients, of which one is about double the quantity of the other. Both of them are coagulable by heat; and on this account the whole albuminous ingredient of the plasma solidifies when exposed to a boiling temperature. But one of them is coagulable also by magnesium sulphate added in excess. This substance is termed *metalbumen*, and is present in the plasma in the proportion of about 22 parts per thousand. It may be separated from the remainder by filtering the plasma through magnesium sulphate, which retains the metalbumen in a coagulated form and allows the remaining liquid to pass through. The second substance, which has passed through the filter, and which is coagulable by heat but not by magnesium sulphate, is *albumen* proper. It has been called "serine" by Denis and Robin, to indicate that it is the kind of albumen present in blood-serum. It exists in the plasma in the proportion of about 53 parts per thousand, being accordingly rather more than twice as abundant as the metalbumen. It is not known whether these two substances are mutually convertible, or if so, which of them is produced by transformation of the other.

A certain quantity of *albuminose* is also to be found in the blood, probably derived from the products of digestion. Its quantity, according to Robin, varies from 1 to 4 parts per thousand. As it is absorbed from the intestine during digestion, and neither accumulates in the blood nor appears in any of the excretions, it is no doubt transformed into some other substance after being taken into the blood.

The *fatty matters* exist in the blood mostly in a saponified form, excepting soon after the digestion of food rich in fat. At that period, the emulsioned fat finds its way into the blood, and circulates for a time unchanged. Afterward it disappears as free fat, but remains partly in the saponified condition.

The *saline* substances of the plasma are principally sodium and potassium chlorides, phosphates, and sulphates, together with lime and magnesium phosphates. Of these the sodium chloride is the most abundant, constituting nearly 40 per cent. of all the mineral ingredients. The sodium and potassium phosphates are of great importance in providing for the alkalescence of the blood plasma, a property which is essential to the performance of the functions of nutrition and even to the immediate continuance of life; since it is the alkaline condition of the plasma which enables it to absorb from the various tissues the carbonic acid produced in their substance and return it to the centre of the circulation, for elimination by the lungs. The sodium and potassium carbonates also take part in the production of this alkalescence, and in the herbivorous animals are its principal cause; while in the carnivora the alkaline phosphates alone are to be found in the plasma in appreciable quantity. In the human subject, under the use of an ordinary mixed animal and vegetable diet, both the alkaline phosphates and carbonates are present in varying proportions.

The earthy phosphates of the plasma, which are by themselves insoluble in alkaline or neutral fluids, are held in solution in the blood by union with its albuminous ingredients.

Coagulation of the Blood.

A few moments after the blood has been withdrawn from the vessels, a remarkable phenomenon presents itself, namely, its coagulation or clotting. This process commences at nearly the same time throughout the whole mass of the blood, which becomes first somewhat diminished in fluidity, so that it will not run over the edge of the vessel, when slightly inclined; while its surface may be gently depressed with the end of the finger or a glass rod. It then becomes rapidly thicker, and at last solidifies into a uniformly red, opaque, consistent, gelatinous mass, which takes the form of the vessel in which the blood was received. The process usually commences, in man, in about fifteen minutes after the blood has been drawn, and is completed in about twenty minutes.

The coagulation of the blood is dependent upon the presence of its fibrine. This fact may be demonstrated in various ways. In the first place, if freshly drawn frog's blood be mixed with a solution of sugar, of the strength of one-half per cent., and placed upon a filter, the blood-globules will be retained upon the filter, while a transparent colorless liquid passes through, which after a time coagulates like fresh blood. Secondly, if horse's blood, which coagulates more slowly than that of most other warm-blooded animals, be drawn from the veins into a cylindrical glass vessel and allowed to remain at rest, by the time coagulation

takes place the blood-globules have subsided from the upper part of the fluid, leaving a layer at the surface which is colorless and partly transparent, but which is as firmly coagulated as the rest. Thirdly, if horse's blood be freshly drawn into such a vessel, surrounded by a freezing mixture and kept at the temperature of 0° (32° F.), coagulation is for the time altogether suspended, and the globules sink toward the bottom, leaving a transparent colorless fluid above. If this colorless fluid be removed by decantation, and allowed to rise in temperature a few degrees, it coagulates firmly like fresh blood.

These facts show that the blood-globules take no direct part in the process of coagulation; and that, when present, they are simply entangled mechanically in the solidifying clot.

Finally, if the freshly drawn blood of man, or of any of the warm-blooded animals, be briskly stirred with a bundle of twigs or glass rods, the fibrine coagulates in comparatively small mass upon the surface of the foreign bodies; and the red globules which it entangles may be removed by washing, without changing in any way its essential characters.

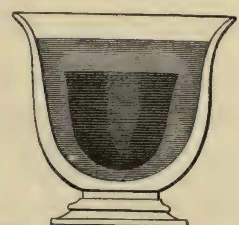
It is the fibrine, therefore, which, by its own coagulation, induces the solidification of the entire blood. As it is uniformly distributed beforehand throughout the blood, when coagulation takes place the minute filaments which make their appearance in it entangle in their meshes the globules and the albuminous fluids of the plasma. A very small quantity of fibrine, therefore, is sufficient to include in its solidification all the fluid and semi-fluid ingredients which were before mingled with it, and to convert the whole into a voluminous, trembling, jelly-like mass of coagulated blood.

Fig. 88.

Bowl of recently COAGULATED BLOOD, showing the whole mass uniformly solidified.

As soon as the coagulum has fairly formed, it begins to contract, increasing somewhat in consistency as it diminishes in size. By means of this contraction the albuminous liquids begin to be pressed out from the meshes in which they were entangled. A few isolated drops first appear on the surface of the clot, which soon increase in size and also become more numerous. After a time they enlarge so much as to come in contact with each other at various points, when they coalesce, extending in all directions as the exudation increases, until the whole surface of the clot is covered with a thin layer of fluid. The clot at first adheres pretty strongly to the sides of the vessel into which the blood was drawn; but as its contraction goes on, its edges are separated, and the fluid continues to exude between it and the sides of the vessel. This process continues

Fig. 89.



Bowl of COAGULATED BLOOD after twelve hours, showing the clot contracted and floating in the fluid serum.

for ten or twelve hours; the clot growing constantly smaller and firmer, and the expressed fluid more abundant.

The globules, owing to their greater consistency, do not escape with the albuminous fluids, but remain entangled in the fibrinous coagulum. At the end of ten or twelve hours the whole of the blood has usually separated into two parts, namely, the *clot*, which is a red, opaque, semi-solid mass, consisting of the fibrine and the blood-globules; and the *serum*, which is a transparent, nearly colorless fluid, containing the water, albumen, and saline matters of the plasma.

The change of the blood in coagulation may be expressed as follows:

Before coagulation the blood consists of

1st. Globules; and 2d. Plasma—containing . . . $\left\{\begin{array}{l}\text{Fibrine,}\\ \text{Albumen,}\\ \text{Water,}\\ \text{Salts.}\end{array}\right.$

After coagulation it is separated into

1st. Clot, containing $\left\{\begin{array}{l}\text{Fibrine and}\\ \text{Globules;}\end{array}\right.$ and 2d. Serum, containing $\left\{\begin{array}{l}\text{Albumen,}\\ \text{Water,}\\ \text{Salts.}\end{array}\right.$

Conditions favoring or retarding Coagulation.—The coagulation of the blood is influenced by various physical conditions. In the first place it is suspended by a freezing temperature. If the blood be drawn into a narrow vessel surrounded by a freezing mixture, so that the whole of it is rapidly cooled down to 0° (32° F.), coagulation does not occur, and the blood remains fluid indefinitely, so long as the temperature is not allowed to rise above this point. A variety of other changes, such as fermentation, putrefaction, and many chemical combinations or decompositions, are also prevented, as it is well known, by special conditions of temperature.

Secondly, the coagulation of the blood is prevented by certain of the neutral salts. If fresh blood be allowed to mingle with a concentrated watery solution of sodium sulphate, no coagulation takes place. This is not because the coagulable material has been decomposed or chemically altered; because if the mixture be diluted with six or seven times its volume of water, so as to reduce the concentration of the saline solution, the fibrine solidifies in a few moments in the usual manner.

Coagulation of the blood may also be hastened or retarded by variations in the manner of its withdrawal from the veins, or in the surfaces with which it afterward comes in contact. If drawn rapidly from a large orifice, it remains fluid for a comparatively long time; if slowly, from a narrow orifice, it coagulates quickly. The shape of the vessel into which the blood is received, and the condition of its internal surface, also exert an influence. The greater the extent of surface over which the blood comes in contact with the vessel, the more is its coagulation hastened. If the blood be allowed to flow into a tall, narrow, cylindrical vessel, or into a shallow plate, it coagulates more rapidly

than if received into a hemispherical bowl, in which the extent of surface is less, in proportion to the quantity of blood which it contains. For the same reason, coagulation takes place more rapidly in a vessel with a roughened internal surface than in one which is smooth; and blood coagulates most rapidly when spread out in thin layers, or entangled among the fibres of cloth or sponges. Hemorrhage, accordingly, continues longer from an incised wound than from a lacerated one; because the blood, in flowing over the ragged edges of lacerated tissues, solidifies upon them, and thus blocks up the wound.

In all cases there is an inverse relation between the rapidity of coagulation and the firmness of the clot. When coagulation takes place slowly, the clot afterward becomes small and dense, and the serum is abundant. When it is rapid, there is but little contraction of the coagulum, an imperfect separation of the serum, and the clot remains large, soft, and gelatinous.

The blood coagulates also in the interior of the vessels *after stoppage of the circulation.* Under these circumstances coagulation takes place less rapidly than if the blood were wholly withdrawn from the body. In man, as a general rule, the blood is found coagulated in the cavities of the heart and large vessels in from twelve to twenty-four hours after death. In the lower animals, coagulation occurs earlier than this, namely, from four to ten hours after death.

Coagulation of the blood takes place also in the interior of the body, during life, from *local arrest or impediment of the circulation.* Thus, if blood be accidentally extravasated into the connective tissue, the substance of the brain or spinal cord, or a serous cavity, it coagulates after a short time, and forms a clot which takes the shape of the cavity occupied by it. If a ligature be placed upon an artery in the living subject, the blood which stagnates above the ligatured spot coagulates as it would do if removed from the circulation. The clot extends from the ligature backward to the situation of the next collateral branch, that is, to the point at which the movement of the circulation still continues. In an arterial aneurism, during life, the blood in the dilated portion of the artery, which is sufficiently removed from the centre of the current, gradually coagulates upon the inner surface of the sac. In these cases, as well within as outside the body, and during life as well as after death, the stoppage or retardation of the circulatory movement induces, after a time, the coagulation of the blood.

It is asserted, however, by some observers, that simple stoppage of the circulation during life will not induce coagulation, unless the inner membrane of the bloodvessels be wounded or irritated. According to Burdon Sanderson, if blood be imprisoned in the jugular vein of the living rabbit by carefully compressing the vessel at two points between transverse needles, so arranged as not to wound or bruise the vascular coats, it will remain fluid in this situation for two days; while if ordinary ligatures be placed immediately around the vessel, a coagulum is formed in the isolated portion of the vein.

The coagulation of fibrine is not a commencement of organization. It is simply the passage of an albuminous ingredient of the blood from its normal fluid condition to a state of solidity. The coagulable ingredient of the blood, when solidified, has lost its natural properties as a constituent of the liquid plasma, and cannot afterward be restored to its original condition. The clot, therefore, when once formed, even in the interior of the system, as in cases of ligature, apoplexy, or extravasation, becomes a foreign body, and is reabsorbed by the neighboring parts during convalescence. At first the clot is comparatively voluminous, soft, and of a deep red color. Its more fluid parts are then reabsorbed, and the clot becomes smaller and denser. The red coloring matter gradually diminishes as absorption goes on, and finally altogether disappears. The time required for complete reabsorption varies from a few days to several months, according to the size of the clot and the situation in which extravasation has taken place.

Nature of the Process of Coagulation.—The difficulty in fully understanding the nature of coagulation depends upon the fact that the blood naturally continues fluid under all ordinary conditions while circulating in the vessels, but coagulates inevitably within a few minutes after its removal. Properly speaking, the fibrine which we obtain at the time of coagulation, either by itself or as forming a part of the clot, does not pre-exist in the blood with the same constitution and properties, otherwise it would coagulate within the vessels during life. It must be derived from some ingredient of the blood, which, on being withdrawn from the current of the circulation, suffers a change by which it becomes spontaneously coagulable. It is not easy to understand what this change may be, or what are the immediate influences which produce it.

There are two theories in existence as to the nature of coagulation. According to one of them (Denis), the coagulable fibrine is produced by the spontaneous decomposition of a liquid substance pre-existing in the blood. This substance is termed *plasmine*, and is thought to be present in the plasma of the blood in the proportion of 25 parts per thousand. When withdrawn from the circulation it decomposes or separates into two new substances. One of these is fibrine (3 parts per thousand), which immediately coagulates; the other is metalbumen (22 parts per thousand), which remains fluid. The basis of this theory is, that if fresh blood be drawn into a concentrated solution of sodium sulphate, as above stated, no coagulation takes place. But if sodium chloride in powder be added to this mixture in the proportion of ten per cent., it precipitates a white pasty substance, which is thrown down because it is insoluble in a sodium chloride solution of that strength. This substance, the so-called "plasmine," represents 25 parts per thousand of the original plasma. After its separation it may be readily dissolved again by the addition of water; but in a few moments its solution coagulates, yielding 3 parts of a solid matter like ordinary fibrine, and 22 parts of a liquid substance having the properties of metalbumen. The albumen proper of the blood remains behind in the sodium sulphate

solution, not having been precipitated by the addition of sodium chloride.

According to the other theory (Schmidt), the coagulable fibrine is produced by the union of two previously existing substances, neither of which is coagulable by itself. One of these is termed *fibrino-plastic matter*, because it has the property of inducing coagulation in a liquid containing the other material. This second material is named *fibrinogen*, being considered as more directly the generator of the coagulable fibrine. The plasma of the blood is supposed to contain both these substances, but in very different quantities; the fibrino-plastic matter being abundant, the fibrinogen comparatively scanty. When the fibrinogen, accordingly, has all been converted into fibrine and has coagulated, a surplus of fibrino-plastic matter still remains in the serum, and may be used to induce coagulation in other liquids which would not coagulate of themselves. This last fact forms the basis of the theory. If the clear serum from coagulated blood be added, at the temperature of the living body, to filtered hydrocele fluid, after some minutes the mixture coagulates into a transparent gelatinous mass, which afterward exudes a colorless serum. Both fibrino-plastic matter and fibrinogen are obtained from the liquids containing them, by dilution with water and by passing though them for a considerable time a continuous stream of carbonic acid. Fibrinogen is also precipitable by the addition of sodium chloride to the point of saturation.

This theory not having been found sufficient to account for all the phenomena of coagulation, its author has modified it[1] by supposing that, while fibrino-plastic matter and fibrinogen by their combination furnish the material of the coagulable fibrine, they need, in order to effect their union, the influence of a third substance, which does not itself form any part of the fibrine, but which acts as a ferment to excite the combination of the two others. A fluid accordingly may contain both fibrino-plastic matter and fibrinogen, and yet will not coagulate unless the ferment be also present. The ferment is supposed to be generated in the blood only after its withdrawal from the vessels; and this accounts for its fluid condition while the circulation is going on.

Neither of the foregoing explanations rests upon complete demonstration. The plasmine of Denis may be, from the first, a mixture of two different substances, both of which are precipitable by sodium chloride from the sodium sulphate solution; and the union of the two fibrine generators of Schmidt, under the influence of a "ferment," still leaves it quite unknown how or by what causes this ferment is generated when the blood coagulates after removal from the vessels. The only thing which seems absolutely certain is that a substance exists in the blood in small quantity which becomes coagulable by a spontaneous change soon after it is withdrawn from the influences of the circulation.

If we endeavor to explain why this change and the consequent coagu-

[1] Archiv für die Gesammte Physiologie, 1872, Band vi. p 413.

lation of the blood do not occur normally in the bloodvessels during life, the most important facts bearing on this point are that the blood of the renal and hepatic veins yields no fibrine, or much less than arterial blood. The substance which causes coagulation, therefore, *is decomposed and disappears from the blood while passing through the liver and the kidneys.* This is established by the observations of Simon, Lehmann, and Brown-Séquard. While an abundance of fibrine may be obtained from either arterial or portal blood, none or only feeble traces of it are to be found in that of the hepatic or the renal veins. This substance, being constantly eliminated from the blood in this way by the liver and kidneys, is necessarily produced afresh elsewhere at the same time, since its quantity in the blood remains unchanged; and the new material thus formed is also rapidly altered by a continuation of the same process. By calculating approximately the quantity of blood contained in the whole body and that passing daily through the liver and kidneys, it appears that a quantity of fibrine equal to that in the entire blood must be destroyed and reproduced several times over in the course of a single day. Thus the fibrine which appears in a specimen of blood drawn from the vessels at any one time, and which causes its coagulation, is derived from a substance of very recent formation; and, if allowed to remain in the bloodvessels, it would have disappeared by metamorphosis before arriving at the stage of coagulation.

Usefulness of Fibrine and of its property of Coagulation.—Although the fibrine of the blood, from its small quantity and the general character of its properties, does not seem to take a direct part in the more essential phenomena of nutrition, it is still a very important ingredient of the circulating fluid. Upon the presence of this substance depends the process by which nature effects the arrest of hemorrhage from divided or ruptured bloodvessels. Whenever a wound is accidentally made in vascular tissues, the blood at first flows freely from the external orifice. But a portion of the blood coagulates upon the edges of the wound, and after a time the successive deposits of cogulated fibrine become sufficient to effectually close the opening and prevent further loss of blood. The proper treatment for wounds of moderate size, in which only the veins and capillaries, or small arteries, have been divided, is simply to apply compression and to keep the edges of the wound in contact continuously for fifteen or twenty minutes. By this time the thin layer of blood between the wounded surfaces, thus kept at rest, has coagulated, and the hemorrhage does not reappear when the artificial compression is removed. If a larger artery be opened, the force with which the blood is expelled prevents local coagulation, or is sufficient to detach the coagula after they are formed. In such cases accordingly the surgeon places a ligature upon the wounded artery itself, and in this way effectually controls the hemorrhage. But even in this instance the ligature is only a means of applying compression for a longer time, and is still temporary, as it must come away again when it ulcerates through the coats of the vessel. The immediate and essential means of stopping

the flow of blood, even in a ligatured artery, is the coagulum which forms within the vessel behind the ligature; and which, by the time the ligature is detached by ulceration, has become sufficiently firm and adherent to resist the impulse of the blood.

The importance of fibrine in this respect is shown by the difficulties which follow in cases where it is deficient. In some instances of the ligature of large arteries, in patients much exhausted by injury or by previous loss of blood, the surgeon finds that when the ligature comes away the bleeding begins again, no internal clot having been formed; and a second ligature, applied above the situation of the former one, is again followed by secondary hemorrhage. In certain persons also there appears to be a congenital deficiency of the coagulating ingredient of the blood, a peculiarity sometimes observed in several members of the same family; and in these cases, any slight accidental wound, or trivial surgical operation, may be followed by long-continued or even fatal hemorrhage.

Entire Quantity of Blood in the Body.—The estimation of the whole mass of the blood in the living body is surrounded with many difficulties. The first and simplest method adopted for this purpose was by suddenly dividing all the vessels of the neck in the living animal and collecting all the blood which escaped. This method, however, was found to be quite faulty, since the flow of blood ceases, in such an experiment, not because the whole of it has been discharged, but because coagula have formed about the orifices of the divided vessels and because the force of the heart's action is no longer sufficient to overcome the obstruction. A certain quantity of blood, therefore, always remains in the body after death by hemorrhage; and this quantity, as shown by subsequent experiments, may even amount to over 25 per cent. of the whole mass of blood. The animal therefore dies before he has lost quite three-fourths of the circulating fluid.

Other methods have been adopted by various experimenters, none of which are absolutely free from all possible sources of error. The best is that by which, after all the blood is discharged which can be made to escape spontaneously from divided vessels, the circulatory system is immediately injected with water or a weak saline solution, until the fluid of injection, after traversing the vascular channels, returns nearly or quite colorless. The quantity of blood which it has thus washed out of the vessels is then ascertained, either by a comparison of its color with that of a watery dilution of blood of known strength, or by comparing the quantity of its solid ingredients with that of a similar watery dilution.

The most accurate of these processes is that employed by Steinberg,[1] who, after bleeding the animal to death, injected the aorta with a watery solution of sodium chloride, of the strength of one-half per cent., until the fluid of injection returned colorless. The whole of the fluid which

[1] Archiv für die Gesammte Physiologie, 1873, Band vii. p. 101.

had been used for injection being then mingled, a small quantity of it was taken, and the proportion of hemoglobine contained in it determined by the spectroscopic test as follows: Equal quantities of pure blood were placed in two similar test-tubes, and diluted, one of them with pure water, the other with the fluid of injection, until each of them, placed before the slit of the spectroscope, just allowed the green light of the spectrum to become visible. From the relative quantities of the two liquids which must be added to produce this result, the amount of hemoglobine, and consequently of blood, extracted by the injection could be readily calculated. This quantity, added to that which had escaped spontaneously from the vessels, gave the entire amount of blood, as follows:

Quantity of Blood, in various animals, as compared with the weight of the whole body.

In Dogs,	from 8.00	to 8.93	per cent.
" Cats,	" 8.40	" 9.61	"
" Guinea-pigs,	" 8.13	" 8.33	"
" Rabbits,	" 7.50	" 8.13	"

There is evidence, however, that the quantity of blood varies naturally, in the same animal, according to the condition of the system at large, and especially according to that of the digestive process. Steinberg found that in the cat, while fasting, the percentage of blood was reduced from 8.40 to 5.61 per cent. Bernard[1] has observed that if two animals of the same weight, one of which is in full digestion while the other is fasting, be suddenly decapitated, the quantity of blood discharged from the former is much greater than that from the latter. He has also shown that, in a rabbit during digestion, twice as much blood can be withdrawn without causing death, as in one of the same weight but in the fasting condition. The volume of the blood, therefore, contained in the body, fluctuates, within certain limits, with the alternate introduction of nutritious matter by digestion and its expenditure during the interval of fasting.

The most satisfactory determination of the quantity of blood in the human subject is that by Weber and Lehmann.[2] These observers operated upon two criminals who suffered death by decapitation; the methods and results being essentially the same in both cases. In one of them the body weighed before decapitation 60.14 kilogrammes; and the blood which escaped from the vessels at the time of decapitation amounted to 5540 grammes. In order to estimate the quantity of blood which remained in the vessels, the experimenters injected the arteries of the head and trunk with water until it returned from the veins of a pale red or yellow color, collected the fluid thus returned, and ascertained how much solid matter it held in solution. This amounted to

[1] Leçons sur les Liquides de l'Organisme. Paris, 1859, tome i. p. 419.

[2] Physiological Chemistry, Cavendish edition. London, 1853, vol. ii. p. 269.

37.24 grammes, corresponding to 1980 grammes of blood. The result of the experiment is therefore as follows:

Blood which escaped from the vessels	5540	grammes.
" remained in the body	1980	"
Whole quantity of blood in the living body,	7520	"

The blood, accordingly, in these cases amounted to 12.54 per cent. of the entire bodily weight; and the body of a healthy man, weighing 65 kilogrammes (143 pounds avoirdupois) will contain on the average 8127 grammes (18 pounds) of blood.

CHAPTER XIII.

RESPIRATION.

The most constant and striking phenomenon presented by living organisms, both animal and vegetable, is the absorption of oxygen. A supply of this substance, either in the gaseous form as a constituent part of the atmospheric air, or dissolved in water or other liquids, is indispensably requisite for the maintenance of life and the manifestation of vital phenomena. Oxygen exists diffused everywhere over the surface of the earth, forming rather more than one-fifth part of the volume of the atmosphere, and it is dissolved in greater or less abundance in the water of springs, rivers, lakes, and seas. Animals and plants, accordingly, whether living in the air or in the water, are surrounded by media in which this substance is constantly present. Even parasitic organisms, inhabiting the interior of other living bodies, and the fœtus during the period of its intra-uterine development, though not immediately in contact with oxygen, are supplied with nutritious fluids which have themselves been exposed to its influence. The function of *respiration* consists in the process by which oxygen penetrates the substance of living organisms, together with the changes which accompany and follow its introduction.

Respiration in Vegetables.—In regard to the phenomena of respiration in vegetables, a distinction is to be made between respiration proper and the absorption of gaseous matter for the production of organic material. It is well known that all green plants, under the influence of the solar light, have the power of absorbing carbonic acid and water, and of partially deoxidizing these substances, to form, with their remaining elements, starch, cellulose, and fat. The oxygen thus separated from its inorganic combinations is exhaled by the plant in a free form; while, as a result of the process, an accumulation of organic material takes place in the vegetable fabric, which increases in substance, and may afterward serve for the nutrition of animal bodies. This accordingly is not a process of respiration, but one of organic production. It is peculiar to vegetables, animals having no power to produce organic material, and therefore depending upon vegetables for their supply of food.

Animals, on the other hand, consume the organic material thus produced, at the same time absorbing oxygen and exhaling carbonic acid and water. In this respect there is an opposition between the actions of animal and vegetable life, by which they stand in a complementary relation to each other. Vegetables produce organic matter by a process of deoxidation; animals consume it with the phenomena of oxidation.

But this apparent opposition between the phenomena of animal and vegetable life only exists because plants have the special power of producing organic matter, by which they become the source of nourishment for the entire living creation. The organic substances so produced do not immediately take part in the more active phenomena even of vegetable life. They are, on the contrary, deposited in a more or less quiescent form, and constitute a reserve material, to be afterward transformed and assimilated by the plant, or consumed by herbivorous animals. In vegetables, as well as in animals, a true respiration also takes place, which is marked in both instances by the absorption of oxygen. The deoxidizing process, by which organic matter is produced, occurs only in green vegetables, and under the influence of the solar light; while the absorption of oxygen is a constant phenomenon, taking place in both green and colorless plants, and in darkness as well as in the light.

The more active phenomena of vegetation, moreover, are immediately dependent upon the absorption of oxygen, and cannot go on without it. When the starch which has been stored up in the seed becomes liquefied and converted into sugar, and the process of germination and growth begins, the absorption of oxygen is necessary to its continuance. This is seen not only in germinating seeds, but also in expanding leaf and flower buds, all of which organs consume in a short period several times their volume of oxygen. The processes of germination, growth, and flowering, as well as the intra-cellular movement of the vegetable plasma, the motions of the sensitive-plant in response to stimulus, and the periodical movements of the leaves in certain other vegetable species, all cease in an atmosphere deprived of oxygen.[1] The function of respiration is accordingly a universal one, and essential to all forms of vital activity.

Organs of Respiration.

The process of respiration takes place very actively in the mammalians and birds, less so in reptiles and fishes; and in these different classes the organs by which it is accomplished vary in size and structure according to the activity of the function itself. Its necessary conditions everywhere are that the circulating fluid should be exposed in some way to the influence of the atmospheric air or of an aerated fluid. The respiratory apparatus, accordingly, consists essentially of a moist and permeable animal membrane, termed the respiratory membrane, with bloodvessels on one side of it, and air or an aerated fluid on the other. The blood and the air, consequently, do not come in direct contact with each other, but absorption and exhalation take place through the respiratory membrane which lies between.

[1] Mayer, Lehrbuch der Agrikultur-Chemie. Heidelberg, 1871, Band i. pp. 91–95.

In most aquatic animals, the respiratory organs have the form of *gills* or *branchiæ;* that is, filamentous prolongations of some part of the integument or mucous membranes, which contain an abundant supply of bloodvessels, and which hang out freely into the surrounding water. In many kinds of amphibious reptiles, as, for example, in *Menobranchus* (Fig. 90), there are upon each side of the neck feathery tufts or prolongations from the mucous membrane of the pharynx, which pass out through lateral fissures in the neck. Each filament consists of a thin fold of mucous membrane, containing in its interior a network of minute bloodvessels. The venous blood, as it enters the filament, is exposed to the influence of the surrounding water, and is thus converted into arterial blood. The apparatus is further supplied with a cartilaginous framework and a set of muscles, by which the gills are kept in motion, and constantly brought into contact with fresh portions of the aerated fluid.

Fig. 90.

HEAD AND GILLS OF MENOBRANCHUS.

In terrestrial and air-breathing animals, the respiratory apparatus is situated internally. In salamanders and newts, for example, which, though partly aquatic in their habits, are air-breathing animals, the lungs are cylindrical sacs, running nearly the entire length of the body, commencing anteriorly by a communication with the pharynx, and terminating by rounded extremities at the posterior part of the abdomen. These air-sacs have a smooth internal surface; and the blood which circulates through their vessels is arterialized by exposure to the air contained in their cavities. The air is forced into the lungs by a kind of swallowing movement, and is after a time regurgitated and discharged, to make room for a fresh supply.

Fig. 91.

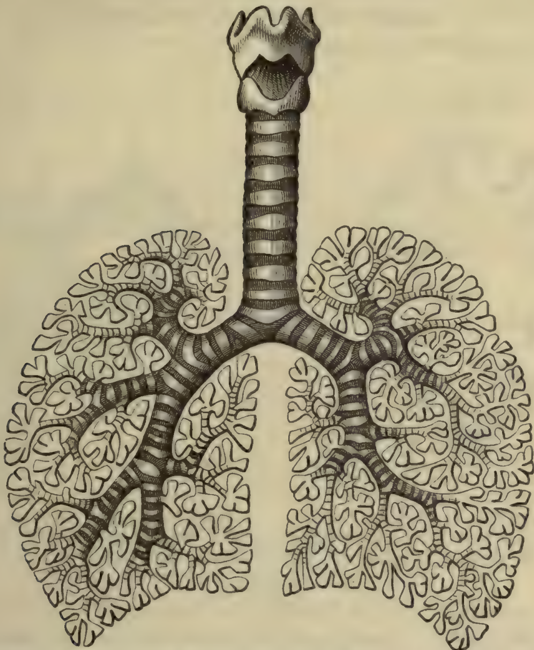
LUNG OF FROG, cut open, showing its internal surface.

In frogs, turtles, and serpents, the cavity of the lung, instead of being simple, is divided by incomplete partitions into a number of smaller cavities or "cells." The cells all communicate with the central pulmonary cavity; and the partitions, which join each other at various angles, are composed of thin, projecting vascular folds of the lining membrane. (Fig. 91.) By this arrangement, the extent of surface presented to the air by the pulmonary membrane is increased, and the arterialization of the blood takes place with a corresponding degree of rapidity.

In man, and in the warm-blooded quadrupeds, the lungs are constructed on a plan essentially similar to the above, but which differs from it in

the greater extent to which the pulmonary cavity is subdivided. The respiratory apparatus in man (Fig. 92) commences with the larynx, which communicates with the pharynx at the upper part of the neck.

Fig. 92.



HUMAN LARYNX, TRACHEA, BRONCHI, AND LUNGS; showing the ramification of the bronchi, and the division of the lungs into lobules.

Then follows the trachea, a membranous tube with cartilaginous rings, which, upon its entrance into the chest, divides into the right and left bronchi. These divide successively into secondary and tertiary bronchi; the subdivision continuing, while the bronchial tubes grow smaller and more numerous, and separate constantly from each other. As they diminish in size, the tubes grow more delicate in structure, and the cartilaginous rings and plates disappear from their walls. They are finally reduced, according to Kölliker, to the size of 0.3 millimetre in diameter; and are composed only of a thin mucous membrane, lined with pavement epithelium, resting upon an elastic fibrous layer. They are then known as the "ultimate bronchial tubes."

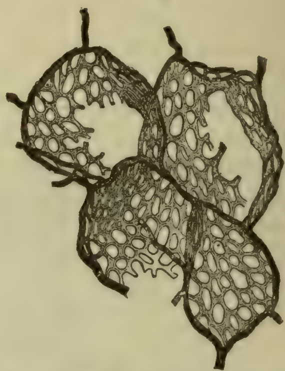
Each ultimate bronchial tube terminates in a pyramidal division or islet of the pulmonary tissue, about 2 millimetres in diameter, which is termed a "pulmonary lobule." Each lobule may be considered as representing the entire frog's lung in miniature. It consists of a vascular membrane in the form of a pyramidal sac, the cavity of which is divided into secondary compartments by thin septa or partitions which project from its internal surface. These secondary cavities are the "pulmonary

vesicles." They have, according to Kölliker, an average diameter of about 0.25 millimetre; but owing to the elasticity of their walls, each vesicle is capable of dilating to double or triple its former size, and returning to its original dimensions when the distending force is removed. There is every reason to believe that during life they are alternately enlarged and diminished in size, as the lungs are filled and emptied with the movements of respiration.

Fig. 93.

SINGLE LOBULE OF HUMAN LUNG.—*a.* Ultimate bronchial tube. *b.* Cavity of lobule. *c, c, c.* Pulmonary vesicles.

Fig. 94.



NETWORK OF CAPILLARY BLOOD-VESSELS in the Pulmonary Vesicles of the Horse. (Frey.)

Each pulmonary vesicle is covered upon its exterior with a close network of capillary bloodvessels, which penetrate into the septa between it and the adjacent cavities, and which are thus exposed on both sides to the influence of the atmospheric air. In the walls of the vesicles, and also in the interspaces between the lobules, there is an abundance of elastic tissue, which gives to the pulmonary structure its property of resiliency. The thin layer of pavement epithelium lining the ultimate bronchial tubes extends into the cavities of the lobules and vesicles, forming, according to the observations of Kölliker, a continuous investment of their internal surface.

The abundant involution of the respiratory membrane, effected by the subdivision of the bronchial tubes and the multiplication of the vascular septa between the vesicles, existing in the lungs of man and the mammalians, evidently increases to an extraordinary degree the functional activity of the organs of respiration. The entire extent of the respiratory surface in the human lungs has been estimated at 130 square metres, which is probably not an exaggeration. The blood, accordingly, in the pulmonary capillaries, distributed in thin layers over so large a surface, in immediate proximity to the air in the cavity of the vesicles, is placed under the most favorable conditions for its rapid and complete arterialization.

Movements of Respiration.

The air which is contained in the pulmonary lobules and vesicles, being used for the purpose of arterializing the blood, becomes rapidly vitiated in the process of respiration, and requires accordingly to be as rapidly expelled and replaced by a fresh supply. This exchange or renovation of the air is effected by alternate movements of the chest, of expansion and collapse, which follow each other in regular succession, and which are known as the "movement of inspiration," and the "movement of expiration."

Movement of Inspiration.—The expansion of the chest is effected by two sets of muscles, namely, the diaphragm and the intercostals. While the diaphragm is relaxed, it has the form of a vaulted partition, the edges of which are attached to the inferior extremity of the sternum, the inferior costal cartilages, the borders of the lower ribs and the bodies of the lumbar vertebræ, while its convexity rises into the cavity of the chest, as high as the level of the fifth rib. When the fibres of the diaphragm contract, their curvature is necessarily diminished; and they approximate a straight line, in proportion to the extent of their contraction. Consequently, the entire convexity of the diaphragm is diminished in the same proportion, and it descends toward the abdomen, enlarging the cavity of the chest from above downward. At the same time the intercostal muscles enlarge it in a lateral direction. For the ribs, articulated behind with the bodies of the vertebræ, and attached to the sternum by the flexible and elastic costal cartilages, are so arranged that, in a position of rest, their convexities look obliquely outward and downward. When the movement of inspiration is about to commence, the first rib is fixed by the contraction of the scaleni muscles, and, the intercostal muscles then contracting simultaneously, the ribs are drawn upward. In this movement, as each rib rotates upon its articulations with the spinal column at one extremity and with the sternum at the other, its convexity is necessarily carried outward at the same time that it is drawn upward, and the parietes of the chest are expanded laterally. The sternum rises slightly with the same movement, and enlarges to some extent the antero-posterior diameter of the

Fig. 95.

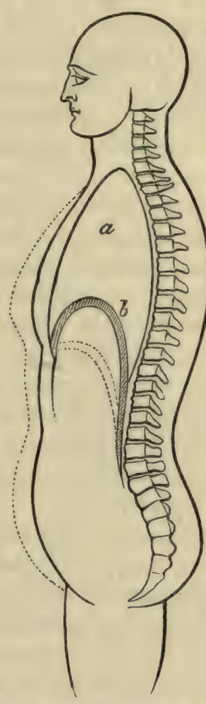


Diagram Illustrating the Respiratory Movements.—*a.* Cavity of the chest. *b.* Diaphragm. The dark outlines show the figure of the chest when collapsed; the dotted lines show the same when expanded.

thorax. By the simultaneous action of the diaphragm which descends, and of the intercostal muscles which lift the ribs and the sternum, the cavity of the chest is expanded in every direction, and the air passes inward, through the trachea and bronchial tubes, by the force of aspiration.

The action of these two sets of respiratory muscles is indicated externally by two different motions, visible to the eye; namely, an expansion of the chest, due to the action of the intercostals, and a protrusion of the abdomen, caused by the descent of the diaphragm. In children, as well as in the adult male, in the ordinary quiescent condition, the diaphragm performs most of the work in the act of inspiration; and the movements of the abdomen are the only ones which are especially marked. Any muscular exertion, however, produces an increased expansion of the chest; and the movement of the ribs, accordingly, becomes more plainly visible after walking or running. In the female the movements of the chest, and particularly of its upper half, are habitually more prominent than those caused by the action of the diaphragm; and this difference in the mechanism of respiration is a characteristic mark of the two sexes.

In certain abnormal conditions the activity of either the intercostal muscles or the diaphragm may be separately suspended, leaving the entire work of respiration to be performed by the remaining set of muscles. If the intercostal muscles be paralyzed, by disease or injury of the spinal cord in the lower cervical or upper dorsal region, the thorax remains quiescent in respiration, while the protrusion of the abdomen is increased in extent to a corresponding degree. This mode of breathing is called *abdominal respiration.*

In cases of peritonitis, on the other hand, or any local inflammation within the abdominal cavity, the movements of the diaphragm are sometimes restrained, owing to the pain which they excite in the inflamed surfaces. This is known as *thoracic respiration;* since the expansion of the chest becomes more active than usual, and is the only visible movement performed.

Movement of Expiration.—After the movement of inspiration is accomplished and the lungs have been filled with air, the diaphragm and intercostal muscles relax, and a movement of expiration takes place, by which the chest is partially emptied, and a portion of the air contained in the pulmonary cavity is expelled. While the movement of inspiration, however, is an active one, accomplished by means of muscular contraction, that of expiration is a passive one, resulting from a combination of several forces. The principal one of these forces is the elastic reaction of the lungs themselves, due to the numerous fibres of elastic tissue which enter into the structure of the walls of the pulmonary vesicles and smaller bronchial tubes, and are disseminated generally between the lobules. The existence of this elastic force in the pulmonary tissue is readily demonstrated by removing the lungs from the chest of a recently killed animal, distending them by artificial

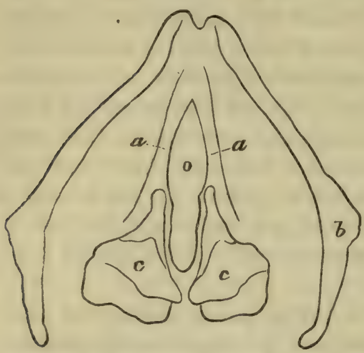
insufflation through a tube inserted into the trachea, and then relieving them from pressure. They at once react with sufficient power to expel the larger portion of the air which had been forced into their cavities. The same elasticity being constantly present during life, the air is subjected to its pressure, and is consequently expelled as soon as the muscles of inspiration cease to act. Other organs, however, aid in the same process. The costal cartilages, which are also elastic, having been twisted slightly out of position by the elevation of the ribs, resume their original form, and, drawing the ribs down again, thus serve to compress the sides of the chest. Lastly, the abdominal organs, which have been displaced by the descent of the diaphragm, are forced backward by the elasticity of the abdominal walls and of their own fibrous attachments, carrying the relaxed diaphragm before them. By the constant recurrence of these alternating movements of inspiration and expiration, fresh portions of air are incessantly introduced into and expelled from the chest.

All the air, however, contained in the lungs, is not changed at each movement of respiration. On the contrary, a considerable quantity remains in the pulmonary cavity after the most complete expiration; and even when the lungs have been removed from the chest, they still contain a certain amount of air, which cannot be entirely displaced by any violence short of disintegrating the pulmonary tissue. It is evident, therefore, that only a comparatively small portion of the air in the lungs passes in and out with each respiratory movement; and it will require several successive respirations before it can be entirely changed. The proportion existing between the air which is changed at each respiration and the entire quantity contained in the chest varies considerably with the different conditions of the respiratory function; but the average results obtained by different observers show that, in general, the volume of the inspired and expired air is from 10 to 13 per cent. of that contained in the whole of the pulmonary cavity. Thus it will require from eight to ten respirations to renovate completely the air in the lungs.

Respiratory Movements of the Glottis.—Beside the movements of expansion and collapse already described, belonging to the chest, there are similar movements of respiration which take place in the larynx. If the respiratory passages be examined in the state of collapse in which they are usually found after death, it will be observed that the opening of the glottis is smaller in calibre than the cavity of the trachea below. The glottis presents the appearance of a narrow chink, while the passage for the inspired air widens in the lower part of the larynx, and in the trachea constitutes a spacious tube, nearly cylindrical in shape, and over 12 millimetres in diameter. We have found that in the human subject the space included between the vocal chords has an area, on the average, of only one square centimetre; while the calibre of the trachea in the middle of its length is 2.81 square centimetres. This disproportion, which is so evident after death, does not exist during life. While

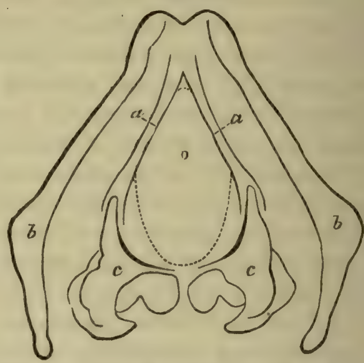
respiration is going on, there is a regular movement of the vocal chords, synchronous with the inspiratory and expiratory movements of the chest, by which the size of the glottis is alternately enlarged and diminished. At inspiration, the glottis opens and allows the air to pass freely

Fig. 96.



HUMAN LARYNX, viewed from above in its ordinary post-mortem condition.—*a.* Vocal chords. *b.* Thyroid cartilage. *c, c.* Arytenoid cartilages. *o.* Opening of the glottis.

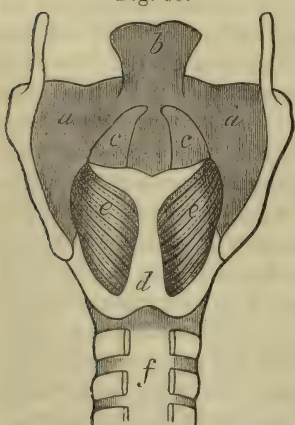
Fig. 97.



The same, with the glottis opened by separation of the vocal chords.—*a.* Vocal chords. *b.* Thyroid cartilage. *c, c.* Arytenoid cartilages. *o.* Opening of the glottis.

into the trachea; at expiration it collapses, and the air is driven out from below. These movements are the "respiratory movements of the glottis." They correspond in every respect with those of the chest, and are excited or retarded by similar causes. Whenever the general movements of respiration are hurried, those of the glottis become accelerated at the same time; and when the movements of the chest are slower or fainter than usual, those of the glottis are diminished in the same proportion.

Fig. 98.



HUMAN LARYNX, POSTERIOR VIEW.—*a.* Thyroid cartilage. *b.* Epiglottis. *c, c.* Arytenoid cartilages. *d.* Cricoid cartilage. *e, e.* Posterior crico-arytenoid muscles. *f.* Trachea.

In the respiratory motions of the glottis, as in those of the chest, the movement of inspiration is an active one, and that of expiration passive. In inspiration, the glottis is opened by contraction of the posterior crico-arytenoid muscles. These muscles originate from the posterior surface of the cricoid cartilage, near the median line; and their fibres, running upward and outward, are inserted into the external angles of the arytenoid cartilages. By the contraction of these muscles, during the movement of inspiration, the arytenoid cartilages are rotated upon their articulations, so that their anterior extremities are carried outward, and the vocal chords stretched and

separated from each other. In this way, the orifice of the glottis may be nearly doubled in size, being increased from 0.94 to 1.69 square centimetre.

At the time of expiration, the posterior crico-arytenoid muscles are relaxed, and the elasticity of the vocal chords brings them back to their former position.

The motions of respiration consist, therefore, of two sets of movements, namely, those of the chest and those of the glottis. These movements, in the natural condition, correspond with each other both in time and intensity. It is at the same time and by the same nervous influence, that the chest expands to inhale the air, while the glottis opens to admit it; and in expiration, the muscles of both chest and glottis are relaxed, while the elasticity of the tissues restores the parts to their original condition.

Rapidity of the Movements of Respiration.—The movements of respiration in the human subject follow each other in general with great regularity, and, according to the results obtained from the most extensive and varied observations, are performed on the average with a rapidity of 20 inspirations per minute. This rate varies considerably under the influence of different conditions, one of the most important of which is age. It is well known that respiration, as a rule, is more rapid in young children than in the adult, and Quetelet has found, as the average of a large number of observations, that in the newly born infant the rate is 44 per minute, and at the age of 5 years 26 per minute; becoming reduced to the standard rapidity of 20 per minute between the ages of fifteen and twenty years. Even in the adult, a condition of rest or activity readily influences the number of respirations; as, according to the same observer, they are less frequent during sleep than in the waking condition. Even a difference in position has been found to have a perceptible effect, the number of respirations being, in the same individual, 19 per minute while lying down, and 22 per minute when standing up.[1] Any especial muscular activity, as the rapid motion of walking or running, at once increases the frequency of respiration, which returns to its ordinary regularity soon after the exertion has ceased.

In all cases the movements of respiration are involuntary in character, and even their acceleration or diminution is regulated by influences beyond our control. It is possible for a short time to increase or retard the rate of respiration, within certain limits, by voluntary effort; but this cannot be done continuously. If we intentionally arrest or diminish the respiratory movements, after a short interval the nervous impulse becomes too strong to be controlled, and the movements necessarily resume their regular frequency. If on the other hand we endeavor to breathe much more rapidly than twenty times per minute, the exertion soon becomes too fatiguing to be continued, and the rate of movement returns to its normal standard. The movements of respiration, accord-

[1] Milne-Edwards, Leçons sur la Physiologie. Paris, 1857, tome ii. p. 483.

ingly, as they are actually performed, in infancy and childhood, during sleep, and for the greater part of the waking condition, when the attention is not directed to them, are purely automatic in character, like the pulsations of the heart, and do not require the expenditure of any voluntary exertion.

Quantity of Air used in Respiration.—Like all the quantitative estimates connected with respiration, that of the volume of air habitually inspired and expired with the breath, varies considerably as given by different observers. The differences incident to the different individuals subjected to observation, and to the conditions of rest or activity, prevent our arriving at an absolutely invariable standard. The average result, however, which most nearly conforms to the truth, as derived from several of the most trustworthy experimenters, as well as from our own observations, is that which gives the amount of air taken into and expelled from the lungs with each inspiration and expiration as 320 cubic centimetres. It is certain that this estimate is not above the reality. If we take, accordingly, eighteen respirations per minute as the mean rapidity between the sleeping and waking hours, this would amount to 5760 cubic centimetres of inspired air per minute, 345,600 per hour, and 8,294,400 cubic centimetres, or 8294.4 litres per day. But as the breathing is increased, both in rapidity and extent, by every muscular exertion, the entire quantity of air daily used in respiration is not less than 10,000 litres, or a little over 350 cubic feet.

The quantity of air daily used in respiration is sometimes employed as a basis for calculating the air-space necessary to allow for each inmate of a hospital or school-room. This estimate alone, however, can never give sufficient data for the purpose. The successful ventilation of a room depends not so much on the quantity of air which it contains at any one time as upon the quantity of fresh air introduced, and of vitiated air expelled, within a certain period. The air of a small room which is thoroughly ventilated may be amply sufficient for respiration, while that of a large room, if allowed to remain stagnant, will gradually become unfit for use. A large air-space, in any occupied apartment, will render ventilation more easy of accomplishment by ordinary methods, because the air will not be so rapidly vitiated by the same number of persons as if it were in smaller volume; but the air must still be changed with a rapidity proportionate to that of its contamination, in order to maintain the apartment in a wholesome condition.

Changes in the Air by Respiration.

The atmospheric air, as it is drawn into the cavity of the lungs, is a mixture of oxygen and nitrogen in the proportion, by volume, of about 21 parts of oxygen to 79 parts of nitrogen. It also contains about .05 per cent. of carbonic acid, a varying quantity of watery vapor, and some traces of ammonia. The last named ingredients, so far as animal respiration is concerned, are quite insignificant in comparison with the oxygen and nitrogen which form the principal part of its mass.

If collected and examined, after passing through the lungs, the air is found to have become altered in the following particulars: first, it has lost oxygen; secondly, it has gained carbonic acid; and thirdly, it has absorbed the vapor of water. The most important of these changes are its diminution in oxygen and its increase in carbonic acid.

Diminution of Oxygen.—According to the researches of Valentin, Vierordt, Regnault, and Reiset, the air loses during respiration, on an average, five per cent. of its volume of oxygen. At each inspiration, therefore, about 16 cubic centimetres of oxygen are removed from the air and absorbed by the blood; and, as we have seen that the daily quantity of air used in respiration is about 10,000 litres, the entire quantity of oxygen thus consumed in twenty-four hours is not less than 500 litres. This is, by weight, 715 grammes, or rather more than one pound and a half avoirdupois.

In consequence of this diminution in oxygen, air which has once been breathed is less capable, both of supporting combustion and of serving for respiration, than before. If an animal be confined in a limited space, the air becomes poorer in oxygen as respiration goes on; and when its proportion has been reduced to a certain point, the animal dies by suffocation, because the substance which is essential to life is no longer present in sufficient quantity. Different kinds of animals are affected in different degrees of intensity by a given diminution in the proportion of atmospheric oxygen. Cold-blooded animals, in which respiration is naturally a comparatively slow process, may continue to breathe when only a very small quantity of oxygen is present; and it has been found that electrical fishes, as well as slugs and snails, may continue respiration until they have completely exhausted the oxygen in the water or the air in which they are confined. But in species where the respiration and circulation are carried on with activity, as in birds, in quadrupeds, and in man, a partial reduction of the oxygen is sufficient to cause death. If the carbonic acid exhaled be absorbed by an alkaline solution, so that the purity of the air be maintained, it is found that a sparrow dies in an hour when its proportion of oxygen has been gradually reduced to 15 per cent.; and a mouse dies in five minutes when the oxygen is reduced to 10 per cent.;[1] the remainder of the air in both cases consisting of nitrogen. In man, also, asphyxia is almost immediately produced when the proportion of oxygen has fallen to 10 per cent.

As a candle flame is also extinguished in an atmosphere deprived of oxygen, this is sometimes employed as a test to determine whether it be safe to enter an atmosphere the composition of which is doubtful. In bread-rooms and beer-vats, where the process of fermentation has been going on, in old wells which have been for a long time closed, or in any newly opened underground cavity or passage, the atmosphere is frequently so poor in oxygen that suffocation would at once follow if

[1] Milne-Edwards, Leçons sur la Physiologie. Paris, 1857, tome ii. p. 638.

they were to be entered without precaution. A lighted candle is accordingly first let down into the suspected cavity, and if a sufficient quantity of oxygen be present, it continues to burn; if not, it is immediately extinguished.

This test is the more valuable, because it is found that the proportion of oxygen necessary to support the combustion of a candle is a little greater than that required for the immediate continuance of respiration. A candle is extinguished when the air contains only 17 per cent. of its volume of oxygen, while a little less than this may still serve a short time for respiration. According to Milne-Edwards, a man may still keep up respiration in an atmosphere which is insufficient to support combustion; and we have repeatedly seen pigeons continue to breathe, though with difficulty, in air in which a candle flame was immediately extinguished.

Although, however, an atmosphere containing from 10 to 17 per cent. of oxygen is not immediately fatal to man by suffocation, it is still unfit for continued breathing. The deficiency is not sufficient to stop respiration at once, but after a time its deleterious effects become manifest, and increase in intensity with each repetition. A complete renewal of the deteriorated atmosphere is essential to the perfect performance of the respiratory process.

The absorption of oxygen by different species of animals varies according to their general state of functional activity; and this difference may be manifested even between species belonging to the same class. Thus it has been found that in the sparrow the amount of oxygen absorbed, in proportion to the weight of the body, is ten times as great as in the common fowl; and in a carp the quantity consumed in the course of an hour would hardly be sufficient for the respiration of a pigeon for a single minute.

In the same individual, also, a temporary increase of muscular activity augments in a marked degree the absorption of oxygen by the lungs. In the human subject it was found by Lavoisier and Seguin that a man, who in the ordinary quiescent condition absorbed a little over 19,000 cubic centimetres of oxygen per hour, consumed nearly 13,000 cubic centimetres of the same gas during fifteen minutes of active muscular exercise; the rapidity of absorption being thus increased to more than $2\frac{1}{2}$ times its former rate. On the other hand, the same process is diminished in activity during sleep; and in the hibernating animals, and in insects which undergo transformation, at the time of their most profound lethargy is reduced to a mere vestige as compared with its usual activity. Spallanzani observed that in insects the amount of oxygen consumed in a given time by the chrysalis was far less than that absorbed before or afterward by the caterpillar or the butterfly; and in the experiments of Regnault and Reiset upon the marmot, at the commencement of the cold season, the consumption of oxygen by this animal was about 500 cubic centimetres per hour for every kilogramme

of bodily weight, while after hibernation was fully established it was reduced to 26 cubic centimetres per kilogramme per hour.

The absorption of oxygen, accordingly, in the process of respiration, is directly associated, so far as regards its rapidity and amount, with the physiological activity of the living organism.

Increase of Carbonic Acid.—The expired air usually contains, in man, about 4 per cent. of its volume of carbonic acid, which it has absorbed in its passage through the lungs. Rather less than 13 cubic centimetres of this gas are accordingly given off with each ordinary expiration; and as we have found that 10,000 litres of air are habitually inhaled and discharged during twenty-four hours, this will give 400 litres of carbonic acid as the amount expired per day. This quantity is, by weight, 786 grammes, or rather less than one pound and three-quarters avoirdupois.

The rate of exhalation of carbonic acid by respiration varies in the same manner and according to the same conditions as the absorption of oxygen. In a general way it may be said, as the result of many trustworthy observations, both in animals and man, that the quantity of carbonic acid exhaled during a given time, in proportion to the weight of the body, is increased by muscular exertion or by any physiological activity of the system, and is diminished by quietude, during sleep, and in a state of inanition.

These facts have been established more particularly for the human subject, in a special series of investigations by Prof. Scharling,[1] who found that the quantity of carbonic acid exhaled was greater during digestion than in the fasting condition. It was greater in the waking state than during sleep; and in a state of activity than in one of repose. It was diminished by fatigue, and by most conditions which interfere with perfect health.

It is also known that in man the habitual rate of exhalation varies according to age, sex, constitution, and development. These variations were very fully investigated by Andral and Gavarret, who found them to be very marked in different individuals, notwithstanding that the experiments were made at the same period of the day, and with the subject as nearly as possible in the same condition. Thus they found that the quantity of carbonic acid exhaled per hour in five different persons was as follows:

Quantity of Carbonic Acid per hour.

In subject No. 1	19,770 cubic centimetres.
" " " 2	15,888 " "
" " " 3	20,475 " "
" " " 4	20,475 " "
" " " 5	26,060 " "

With regard to the difference produced by age, it was found that from the period of eight years up to puberty the quantity of carbonic acid

[1] Annales de Chimie et de Physique. Paris, 1843, tome viii. p. 490.

increases constantly with the age. Thus a boy of eight years exhales, on the average, 9238 cubic centimetres per hour; while a boy of fifteen years exhales 16,168 cubic centimetres in the same time. Boys exhale during this period more carbonic acid than girls of the same age. In males this augmentation of the quantity of carbonic acid continues till the twenty-fifth or thirtieth year, when it reaches, on the average, 22,899 cubic centimetres per hour. Its quantity then remains stationary for ten or fifteen years; then diminishes slightly from the fortieth to the sixtieth year; and after sixty years diminishes in a marked degree, so that it may fall as low as 17,000 cubic centimetres. In one superannuated person, 102 years of age, Andral and Gavarret found the hourly quantity of carbonic acid to be less than 11,000 cubic centimetres.

In women, the increase of carbonic acid ceases at the period of puberty; and its production then remains constant until the cessation of menstruation, about the fortieth or forty-fifth year. At that time it increases again until after fifty years, when it subsequently diminishes with the approach of old age, as in men. Pregnancy, occurring at any time in the above period, produces a temporary increase in the quantity of carbonic acid.

The strength of the constitution, and particularly *the development of the muscular system*, was found to have a great influence in this respect. The largest production of carbonic acid observed was in a young man, 26 years of age, whose frame presented a remarkably vigorous and athletic development, and who exhaled 26,060 cubic centimetres per hour. On the other hand, an unusually large skeleton, or an abundant deposit of adipose tissue, is not accompanied by any similar increase of the carbonic acid.

Andral and Gavarret sum up the results of their investigation as follows:

1. The quantity of carbonic acid exhaled from the lungs in a given time varies with the age, the sex, and the constitution of the subject.

2. In the male, as well as in the female, the quantity of carbonic acid varies according to age.

3. During all periods of life, the male and female may be distinguished by the different quantities of carbonic acid exhaled in a given time. Other things being equal, the male exhales a larger quantity than the female. This difference is particularly marked between the ages of 16 and 40 years, during which period the male usually exhales twice as much carbonic acid as the female.

4. In the male, the quantity of carbonic acid increases constantly from eight to thirty years; and the rate of this increase undergoes a rapid augmentation at the period of puberty. Beyond forty years the exhalation of carbonic acid begins to decrease, and its diminution is more marked as the individual approaches extreme old age, so that near the termination of life, the quantity of carbonic acid produced may be no greater than at the age of ten years.

5. In the female, the exhalation of carbonic acid increases according

to the same law as in the male, from the age of eight years until puberty. But at the period of puberty, at the appearance of menstruation, the exhalation ceases to increase; and it afterward remains stationary so long as the menstrual periods recur with regularity. At the cessation of the menses, the quantity of carbonic acid increases in a notable manner; then it decreases again, as in the male, toward old age.

6. During the whole period of pregnancy, the exhalation of carbonic acid rises, for the time, to the same standard as in women whose menses have ceased.

7. In both sexes, and at all ages, the quantity of carbonic acid is greater, as the constitution is stronger and the muscular system more fully developed.

The process of respiration is not altogether confined to the lungs, but the discharge of carbonic acid takes place also, to a slight extent, both by the urine and the perspiration. Morin[1] has found that the urine always contains gases in solution, of which carbonic acid is considerably the most abundant. The mean result of fifteen observations showed that urine excreted during the night contains about 1.96 per cent. of its volume of carbonic acid. During the day the quantity of this gas contained in the urine varied considerably, according to the condition of muscular repose or activity; since after remaining quiet for an hour or two, it was only 1.19 per cent. of the volume of the urine, while after continued exertion for the same space of time, not only was the urine augmented in quantity, but the proportion of carbonic acid contained in it was nearly doubled, amounting to 2.29 per cent. of its volume.

An equal or even greater activity of gaseous exhalation takes place by the skin. It has been found, by inclosing one of the limbs in an air-tight case, that the air in which it is confined loses oxygen and gains carbonic acid. From an experiment of this sort, Prof. Scharling estimated that the carbonic acid given off from the whole cutaneous surface, in man, is from one-sixtieth to one-thirtieth of that discharged during the same period from the lungs. In the more recent and complete observations of Aubert upon this subject, the whole body without clothing was confined in an air-tight case, leaving only the head exposed. A continuous ventilation of the space was kept up during the course of the experiment with air free from carbonic acid, while the carbonic acid exhaled from the surface of the body was absorbed by baryta-water. Each observation lasted for two hours, and the average result obtained was that, for the entire day of twenty-four hours, 198 cubic centimetres of carbonic acid were exhaled from the skin; a quantity representing rather less than 0.5 per cent. of that given off by the lungs in the same time.

In the amphibious reptiles, as frogs, newts, and salamanders, which

[1] Recherches sur les Gaz libres de l'Urine. Journal de Pharmacie et de Chimie. Paris, 1864, tome xlv. p. 396.

breathe by lungs, and yet can remain under water for a considerable time, the thin, moist, and flexible integument takes a still more active part in the process of respiration. The skin in these animals is covered, not with dry cuticle, but with a delicate layer of epithelium. It accordingly presents all the conditions necessary for the accomplishment of respiration; and while the animal remains beneath the surface of the water, though the lungs are in a state of comparative inactivity, the exhalation and absorption of gases continue to take place through the skin, and respiration goes on without interruption.

Relation between the Oxygen absorbed in respiration and the Carbonic Acid given off.—It has been seen that, in the human subject, with each respiration, on the average, 16 cubic centimetres of oxygen are taken into the system by absorption, and 13 cubic centimetres of carbonic acid given off. As the oxygen thus taken in weighs rather less than .023 gramme, while the carbonic acid discharged weighs .025 gramme, it is evident that the gross result of the process is a loss of weight to the system, and this loss of substance by continued respiration amounts on the average to a little over 70 grammes per day. This is one of the most important facts connected with the physiology of respiration. It shows that this function is carried on at the expense of the substance of the animal body, since the oxygen and carbon discharged under the form of carbonic acid, weigh more than the oxygen which is absorbed in a free state. This difference in quantity must accordingly be supplied in some way by the ingredients of the food; and if this be withheld, the progress of respiration alone will be sufficient to diminish gradually the weight of the body, and to bring it to a state of more or less complete emaciation.

If we endeavor to ascertain what becomes of the oxygen itself, it is found that the quantity of this gas which disappears from the inspired air is not entirely replaced in the carbonic acid exhaled; that is, there is less oxygen in the carbonic acid which is returned to the air by expiration than has been lost by it during inspiration.

The proportion of oxygen which disappears in the interior of the body, over and above that returned in the breath under the form of carbonic acid, varies in different kinds of animals. In the herbivora it is about 10 per cent. of the whole amount of oxygen inspired; in the carnivora, 20 or 25 per cent.; and even in the same animal, the proportion of oxygen absorbed, to that of carbonic acid exhaled, varies according to the kind of food upon which he subsists. In dogs, while fed on meat, according to the experiments of Regnault and Reiset,[1] 25 per cent. of the inspired oxygen disappeared in the body of the animal; but when fed on starchy substances, all but 8 per cent. reappeared in the expired carbonic acid. Under some circumstances, a difference may show itself in the opposite direction; that is, more oxygen may be contained in the carbonic acid exhaled than is absorbed in a free state from

[1] Annales de Chimie et de Physique, tome xxvi. p. 428.

the atmosphere. In some of the experiments of Regnault and Reiset,[1] where rabbits and fowls had been fed exclusively upon bread and grain, the proportion of oxygen in the expired carbonic acid was 101 or 102 per cent. of that taken in by respiration; and even in the human subject, according to the observations of Doyère, the quantity of oxygen eliminated by the breath as carbonic acid, may be considerably greater than that absorbed. But, as a general rule, it is the reverse; the quantity of oxygen which is not to be accounted for in the expired carbonic acid being habitually greater in the carnivorous animals than in the herbivora.

These facts have been established by direct observation, and without any reference to the supposed manner in which the internal changes of respiration take place. Nevertheless, they are susceptible of so ready an explanation that there can be little doubt as to their significance. The simplest case for examination would be that of an herbivorous animal living exclusively upon the carbo-hydrates, as starch or sugar. Since these substances, as their name implies, already contain hydrogen and oxygen in the proportions to form water, any further oxidation which they undergo must result in the production of carbonic acid; and in this case exactly the same quantity of oxygen as that taken in must necessarily be returned to the atmosphere as a constituent of the carbonic acid exhaled; the remainder of the substance being separated from its combinations in the form of water. This process is represented in the following formula:

$$\underset{\text{Starch.}}{C_6H_{10}O_5} + O_{12} = \underset{\text{Carbonic acid.}}{C_6O_{12}} + \underset{\text{Water.}}{H_{10}O_5}.$$

In an animal supported upon this food, therefore, the whole of the oxygen taken in by respiration would reappear in the expired carbonic acid. But in an animal feeding also upon fatty substances, the proportions would be changed. As these matters no longer contain oxygen in the requisite quantity to form water with the hydrogen present, more oxygen must be taken in with the breath than is sufficient to unite with the carbon under the form of carbonic acid; and consequently a portion of it will disappear from the gaseous products of respiration. The change in this instance is as follows:

$$\underset{\text{Oleine.}}{C_{57}H_{104}O_6} + O_{160} = \underset{\text{Carbonic acid.}}{C_{57}O_{114}} + \underset{\text{Water.}}{H_{104}O_{52}}.$$

In effecting, therefore, the complete disappearance of a fatty substance, 160 parts of oxygen will be absorbed, and only 114 parts returned in the form of carbonic acid. This will also take place where albuminous matters are used as food, since it is known that all the nitrogen of these substances is expelled from the body under the form of urea; and after the separation of urea from albumen, a body must be left which is analogous in composition to fat; that is, which contains

[1] Annales de Chimie et de Physique, tome xxvi. pp. 409–451.

less oxygen than would be required to convert all its hydrogen into water.

It is no doubt for these reasons that, in herbivorous animals, feeding largely on the carbohydrates, the quantity of oxygen exhaled in the carbonic acid should be nearly equal to that taken in with the breath; while in the carnivora, which consume only fats and albuminous matters, a larger proportion of oxygen should disappear from the products of respiration.

Finally, some kinds of vegetable food, as fruits and green tissues, contain certain substances in which the oxygen is more than sufficient to form water with the hydrogen present. Such are the salts of vegetable acids, like oxalic, citric, gallic, malic, and tartaric acid. The result of the internal consumption of tartaric acid, for example, would be as follows:

$$\underset{\text{Tartaric acid.}}{C_4H_6O_6} + O_5 = \underset{\text{Carbonic acid.}}{C_4O_8} + \underset{\text{Water.}}{H_6O_3}.$$

In this instance more oxygen will be exhaled, in the carbonic acid produced, than was absorbed from the atmosphere; because a superabundance already existed in the material used as food.

The relative proportions of oxygen and carbonic acid, absorbed and expired in respiration, will therefore vary, as has been well shown by Mayer,[1] not only with the nature of the food, but also according to the transformations, in the interior of the living organism, of one nutritive substance into another, as of a carbohydrate into a fat, or of either into an organic acid. In the fermentation of a saccharine solution there is even an elimination of carbonic acid without the absorption of any oxygen whatever; this process being one, not of direct oxidation, but of the rearrangement of the elements already present in the sugar, a portion of them being exhaled as carbonic acid, while the rest remain behind in the form of alcohol.

In the animal body the function of respiration consists, first in the absorption of oxygen, and secondly in the exhalation of carbonic acid. It is evidently, therefore, so far as its consequences are concerned, an act of oxidation. But the elements of the food are in no case subjected to immediate oxidation. They are digested in the alimentary canal and taken up into the circulating fluid under other forms of organic combination. These undergo still further transformations, both in the blood and in the tissues, passing through a series of successive metamorphoses, until they finally leave the body, principally under the forms of urea, carbonic acid, and water. Oxidation, accordingly, as it occurs in the living body, is not so much the immediate process as the result of the vital operations, and is very different from the direct combustion of hydrocarbonaceous matters in the atmosphere.

Exhalation of Watery Vapor in Respiration.—The watery vapor, exhaled with the breath, is given off by the pulmonary mucous mem-

[1] Lehrbuch der Agrikultur-Chemie. Heidelberg, 1871, p. 101.

brane, by which it is absorbed from the blood. At ordinary temperatures it is transparent and invisible; but in cold weather it becomes partly condensed on leaving the lungs, and appears under the form of a cloudy vapor in the breath. According to the researches of Valentin, the average quantity of water exhaled from the lungs is about 500 grammes per day.

The exhalation of watery vapor by the lungs is a purely physical process, dependent upon the moist and permeable structure of the pulmonary mucous membrane and the volatility of the watery fluid, by which it necessarily becomes vaporized under the requisite conditions of temperature at the ordinary pressure of the atmosphere. Any moist animal membrane, after death as well as during life, loses water by evaporation and thus becomes gradually desiccated. Experiments upon recently killed frogs have shown that the spontaneous desiccation goes on rapidly at first, and afterward more slowly, as the proportion of water contained in the tissues becomes diminished. In the lungs of a warm-blooded animal during life all the requisite conditions are present for rapid and continuous evaporation, namely, a moderately elevated temperature, a constant renewal of atmospheric air by the movements of respiration, and a continuous supply of fresh moisture to the pulmonary membrane by the blood circulating in its vessels. The quantity of watery vapor exhaled by the lungs in a given time is therefore increased or diminished by corresponding changes in the rapidity of respiration, by greater dryness or humidity of the atmosphere, and by increase or diminution of the pulmonary circulation.

In some species of animals, as in the dog, where the integument is comparatively destitute of perspiratory glands, the pulmonary transpiration becomes much more active; and it is not uncommon to see these animals, in hot weather, lying at rest with their tongues protruded, and the movements of respiration doubled or trebled in frequency, for the purpose of increasing the watery exhalation from the lungs.

In the human subject the precise physiological value of the pulmonary transpiration is not known. Though subject to fluctuations according to variation in the physical conditions above mentioned, it is a continuous process, and even at ordinary temperatures the expired breath directed upon a polished glass or metallic surface will always produce an immediate dimness by the condensation of its watery vapor. It is very possible that the vapor thus exhaled, beside being complementary to the perspiration by the skin, may serve as a vehicle for the discharge of certain other substances from the pulmonary cavity.

Exhalation of Organic Matter by the Breath.—Beside carbonic acid and water, the expired air also contains a small amount of an organic ingredient, which communicates a faint but perceptible odor to the breath. This substance is discharged in the vaporous form, probably entangled in the watery vapor exhaled by respiration. Under ordinary circumstances it is present in so small a quantity as to be hardly noticeable; but if a large number of persons be confined in a small apartment

with insufficient ventilation, the organic matter accumulates in the atmosphere, and after a few hours its odor becomes exceedingly offensive. According to Carpenter, if the fluid condensed from the expired air be kept in a closed vessel at ordinary temperatures, a putrescent odor is after a time exhaled, which could only come from some organic substance in a state of decomposition.

When perfectly fresh and in the healthy condition, the organic ingredient of the expired breath is not offensive and appears to have no unwholesome qualities. It is only when accumulated in undue quantity, and allowed to stagnate in the atmosphere, that its disagreeable properties become manifest. It appears to be distinct in character for each species of animal, and it is liable to be absorbed and retained for a time by any porous material, as wood, rough plaster, or woven fabrics. It is easy to distinguish by its odor the breath of cattle from that of sheep or swine, and the odor remains perceptible in any small inclosure or transportation-car in which these animals have been recently confined. The organic ingredient of the expired air which communicates these qualities to the breath has not been isolated in sufficient quantity to determine its exact composition.

Vitiation of the Air by Continued Respiration.—From what has preceded it is seen that the air, after being exhaled from the lungs, has become altered in its constitution by diminution of its oxygen and the addition of certain other materials derived from the breath. Under ordinary conditions, this deteriorated air is at once diffused in the surrounding atmosphere, rising to a higher level on account of its increased temperature, and being readily dispersed by the aerial currents which are always more or less in motion; so that a fresh supply of air, with its normal constitution, is taken into the lungs with each successive inspiration. But when breathing is carried on in a confined space, the air necessarily becomes vitiated; and this effect is produced with rapidity in proportion to the small extent of the air space and the number of men or animals confined in it.

This vitiation of the atmosphere by respiration is accordingly the result of several different changes taking place at the same time, and its effects are a combination of those due to all these alterations.

So far as regards immediate danger to life, the *diminution of oxygen* is no doubt the most important change in the vitiated air, when carried to a sufficient extent. We have already seen that for man and the mammalians, the air is completely irrespirable when its proportion of oxygen is diminished to 10 per cent. In these experiments, however, the carbonic acid exhaled was removed, as fast as produced, by the action of an alkaline solution, so that the air was retained in a state of purity except for its loss of oxygen. In the experiments of Leblanc, a dog and a pigeon, breathing in a confined space, were both reduced to extremities when the air still contained 16 per cent. of oxygen but was also contaminated with 30 per cent. of carbonic acid. The different

modifications of the atmosphere in respiration, therefore, react upon each other and combine to produce a common result.

The second element in the vitiation of the respired air is that due to the presence of *carbonic acid*. The effect of this gas, as produced by respiration, cannot be ascertained from that of an atmosphere consisting of carbonic acid alone. A man or an animal, introduced suddenly into an atmosphere of pure carbonic acid, as sometimes happens in beer-vats and old wells, dies at once by suffocation. But this result is not due to the influence of carbonic acid. It is simply the consequence of the absence of oxygen; and death would take place as promptly, in the warm-blooded animals, by exposure to an atmosphere of pure nitrogen or any other indifferent gas. It may be said that, as a general rule, for birds and small mammalians, the atmosphere becomes incapable of supporting life when, in addition to its normal proportion of oxygen, it contains 20 per cent. of its volume of carbonic acid; that is, five times as much as is present, in man, in the expired breath. But Regnault and Reiset found that dogs and rabbits could continue to breathe without difficulty in an atmosphere containing even 23 per cent of carbonic acid, provided its proportion of oxygen were at the same time increased to 30 or 40 per cent. Thus a part at least of the influence of carbonic acid, when present exclusively or in large quantity in the atmosphere, is evidently due to its physical action in excluding or interfering with the absorption of oxygen.

When pure carbonic acid is gradually mingled with atmospheric air, its immediate effects are not so fatal as they have sometimes been represented. If a pigeon be confined in a glass receiver with a wide open mouth, and carbonic acid be introduced through a tube placed just within the edge of the vessel, so that it will not completely displace the air but gradually mingle with it, its effect is to produce a rapid and laborious respiration, gradually increasing in intensity; and in a few moments the pigeon falls in a state of complete insensibility. But if the glass receiver be removed and fresh air allowed access, the insensibility rapidly passes off, and in a few moments longer the animal is again breathing in a natural manner, without having suffered any perceptible permanent injury. The effect of carbonic acid alone, thus mingled with the atmosphere, is very similar to that of an anæsthetic vapor, like ether or chloroform, with the addition of strong symptoms of dyspnœa.

There is evidence that in man the immediate effects of carbonic acid in respiration are of a similar nature. From personal experiments upon this subject we have found that the inhalation of pure carbonic acid from a gasometer is at first extremely difficult, owing to the stimulant effect of the gas upon the mucous membrane of the larynx, which produces a spasmodic stricture of the glottis. If the gas, however, be allowed to remain in contact with the mucous membrane for a short time, this effect passes off, the glottis may be gently opened, and the carbonic acid drawn into the lungs, by a full, deep inspiration, to the

amount of from 800 to 1200 cubic centimetres. At first it produces in the chest only a sensation of warmth and moderate stimulus. But at the end of two or three seconds there comes on very suddenly a sense of extreme dyspnœa, with rapid and laborious respiration, accompanied immediately by dimness of vision, slight confusion of mind, and partial insensibility, all of which are soon terminated, as respiration returns to its normal condition, leaving only a feeling of quietude and tendency to sleep.

Notwithstanding, however, the intense feeling of dyspnœa produced by such an inhalation of pure carbonic acid, the external signs of actual suffocation are very slight, and bear no proportion to the severity of the sensations. They are confined to a little suffusion of the face with partial lividity of the lips; and the pulse is but little if at all affected.

A mixture of carbonic acid and atmospheric air in equal volumes produces a perceptible feeling of warmth and pungency at the glottis, but may still be readily drawn into the lungs. After two or three deep inspirations, the strong sense of want of air, and the access of rapid and laborious respiration, come on as before. The dyspnœa, suffusion of the face, and lividity are all less marked than after breathing pure carbonic acid, but the subsequent condition of quiescence and partial anæsthesia is more decided and of longer continuance.

A mixture of one volume of carbonic acid with three volumes of atmospheric air may be inspired without difficulty, producing a rather agreeable sensation by contact with the lungs. After about 3000 cubic centimetres have been inhaled in successive inspirations, a sense of dyspnœa comes on, which however is not particularly increased by continuing the inspiration of the mixture to 6000 cubic centimetres. The nervous symptoms produced are moderate in degree, but similar to the preceding.

On the other hand, pure nitrogen has no taste or odor, nor does it have any stimulating effect on the mucous membrane. It may be inspired from the gasometer to the amount of 6000 cubic centimetres, without producing any sense of dyspnœa, or any perceptible effect on the nervous system.

These results indicate that the presence of carbonic acid in the lungs acts as a stimulus to respiration by causing a sense of the want of air; and that furthermore its principal toxic effect, when in abnormal quantity, is that of producing more or less insensibility or anæsthesia. The sense of drowsiness and inattention experienced by an audience in an imperfectly ventilated lecture-room or theatre is probably due to this cause, especially as the burning gas-lights are at the same time contributing to the formation of carbonic acid. The temporary nature of these sensations, and their immediate relief on coming into the open air, are matters of common observation.

The third element in the vitiation of air by the breath is the accumulation of its *organic vapor*. This is the least understood, but probably the most deleterious ingredient of the atmosphere produced by respira-

tion in a crowded and ill-ventilated apartment. It is this which causes the offensive odor and the sense of oppression on entering any confined space, where too great a number of persons have remained for a time without sufficient renewal of the air. It is most marked when such continued respiration and neglect of ventilation have been going on over night, as in a crowded dormitory or sleeping-car; since the organic emanations have then had time not only to accumulate but also to pass into a state of incipient decomposition. They are then in the condition in which they belong to the class of animal poisons; and there is reason to believe that, once introduced into the system, they may cause disturbances which last for a considerable time. It is certain that the contagion of many febrile diseases, as scarlatina, mealses, and smallpox, is communicated through the air by the products of respiration; and the normal organic exhalations of the pulmonary mucous membrane, when altered by concentration, the accumulation of moisture, and an elevated temperature, are undoubtedly capable of producing morbid effects of an analogous kind.

All the above causes of vitiation of the atmosphere in respiration, notwithstanding the differences in their nature and effects, are to be obviated by the same means; that is, a sufficient renewal of the air by ventilation.

Changes in the Blood by Respiration.

The blood as it circulates in the arterial system has a bright scarlet color; but as it passes through the capillaries it gradually becomes darker, and on arriving in the veins it is deep purple, or in some situations nearly black. There are, therefore, two kinds of blood in the body; arterial blood, which is of a bright color, and venous blood, which is dark. The dark-colored venous blood, which has been thus altered by passing through the capillaries, is incapable, in this state, of supplying the organs with their healthy stimulus and nutrition, and has lost its value as a circulating fluid. It is accordingly returned to the heart by the veins, and is thence sent, through the pulmonary artery, to the lungs. In passing through the pulmonary circulation it reassumes its scarlet hue, and is again converted into arterial blood. Thus the most striking physical effect produced upon the blood by respiration is its change of color from venous to arterial.

This change is accomplished by the influence of the air in the pulmonary cavities. For if defibrinated venous blood, recently drawn from the veins of the living animal, be shaken up in a glass vessel with atmospheric air, it at once changes its color and acquires the bright hue of arterial blood. If injected through the vessels of the lungs themselves after removal from the body, the lungs being filled with air, the same change takes place. If a dog be rendered insensible by a narcotic injection or other similar means, the thorax opened, and artificial respiration kept up by the nozzle of a bellows inserted into the trachea, the dark venous blood can be seen in the great veins and in the right

auricle of the heart, while that returning from the lungs to the left auricle is bright red. But if artificial respiration be stopped, the circulation through the lungs continuing, the blood soon ceases to be arterialized in the pulmonary capillaries, and returns to the left auricle of a dark venous hue. On recommencing artificial respiration, arterialization of the blood is again produced, and its red color is restored in the pulmonary veins and the left cavities of the heart.

At the same time, in passing through the pulmonary circulation, the blood undergoes a change in its gaseous constituents, the converse of that which is produced in the air; that is, it absorbs oxygen and exhales carbonic acid.

Passage of Oxygen into the Blood in Respiration.—The oxygen which is absorbed from the air in the lungs is taken up by the blood circulating in the pulmonary capillaries. It does not at once enter into intimate chemical union with other elementary substances, but is still in the form of solution or of such loose combination that it may be removed from the blood by means of the air-pump, by a current of hydrogen or nitrogen, and especially by the action of carbonic oxide (CO), which expels it completely. According to a large number of observations which have been made on this point, its quantity, in the fresh arterial blood of the dog, may vary from a little over 10 per cent. to 22 per cent. of the volume of the blood; the average in the experiments of Schoeffer and Ludwig[1] being about 15 per cent.

Nearly the whole of the oxygen is taken up by the *blood-globules;* the hemoglobine of which has been shown to possess so remarkable a power of absorption for this gas that one gramme of hemoglobine in solution will absorb more than one cubic centimetre of oxygen. According to the experiments of Magnus, while the blood contains more than twice as much oxygen as water could hold in solution at the same temperature, the serum alone has no more solvent power for this gas than pure water; and on the other hand, defibrinated blood, that is, the serum and globules mingled, dissolves as much oxygen as the fresh blood itself. Pflüger also found, as the average of six observations on the arterial blood of the dog, that the oxygen contained in the entire blood was, by volume, 15.6 per cent., while in the serum alone he found only 0.2 per cent. According to the same observer, the arterial blood in the carotids contains nearly though not quite all the oxygen it is capable of holding in solution; since a specimen of dog's blood drawn directly from the artery already contained 18.8 per cent. of oxygen, and after being shaken up with atmospheric air contained rather less than 20 per cent. The blood, therefore, either does not become fully saturated with oxygen in passing through the lungs, or else a little of this gas has already passed into some other form of combination on reaching the carotid arteries.

The color of the blood *depends solely on the presence or absence of oxygen*, not on that of carbonic acid. Venous blood, shaken up with

[1] Archiv für die Gesammte Physiologie, 1868, Band 1, p. 279.

oxygen or atmospheric air, at once assumes the arterial tint, although its carbonic acid may remain. According to Pflüger's experiments, if defibrinated dog's blood be placed in two flasks, and shaken up, one with pure oxygen, the other with a mixture of oxygen and carbonic acid, both specimens will present the same bright color; both of them being found on analysis to contain nearly the same quantities of oxygen, while their proportions of carbonic acid are very different. Also the recently drawn blood of these animals, after they have been made to breathe either pure oxygen, or oxygen and carbonic acid mingled, is of the same color in each instance; the percentage of oxygen which it contains being the same, but that of carbonic acid being different in the two cases.

It is the oxygen, therefore, which, on being taken up by the blood-globules, changes their color from dark purple to bright red. It passes off with the arterial blood in this condition, and is then distributed to the capillary circulation. Here, as the blood comes in contact with the tissues, its oxygen in great measure disappears, and its color is again changed from arterial to venous.

The loss of oxygen by the blood, in traversing the capillaries, is due to its transfer from the blood-globules to the substance of the tissues. Nearly all the tissues, in fact, exert an absorbent power upon oxygen, when exposed to this gas or to atmospheric air containing it. The experiments of Paul Bert[1] have shown that the following tissues, extracted from the body of the recently killed dog and exposed to the contact of atmospheric air in closed vessels, absorb oxygen, with different degrees of intensity, in the following order, namely: muscles, brain, kidneys, spleen, testicle, and pounded bones. Of these the muscles are the most active, absorbing 50 cubic centimetres of oxygen for every 100 grammes of muscular tissue; while the bones absorb only a little over 17 cubic centimetres for the same weight of substance.

The tissues have even a greater absorbent power for oxygen than the blood-globules themselves. This is shown by the experiments of Spallanzani, and still more completely by those of Bert. In these experiments, three equal portions of recently drawn defibrinated dog's blood are placed in test-tubes, a piece of fresh muscular tissue from the same animal being introduced into one of them, a portion of the spleen-tissue into another, while the third is left to itself. After a time it is found that the solid tissues have abstracted oxygen from the blood with which they are in contact, so that in these two specimens the blood, on analysis, contains less oxygen than in the third specimen, which has remained by itself. The result obtained by Bert was as follows:

QUANTITY OF OXYGEN BY VOLUME REMAINING IN

Blood left to itself	18 per cent.
Blood containing spleen tissue . . .	12 "
Blood containing muscular tissue . .	6 "

[1] Leçons sur la Physiologie comparée de la Respiration. Paris, 1870, p. 46.

Finally, successive analyses of the blood, as it passes from the arterial into the venous system, shows that it loses oxygen in proportion as it has been subjected to the influence of the capillary circulation. Bernard[1] found that the blood of the same dog, from different parts of the circulatory system, yielded, by the action of carbonic oxide, the following quantities of oxygen:

Quantity of Oxygen by Volume in	
Arterial blood	18.93 per cent.
Venous blood from right side of heart . . .	9.93 "
Venous blood from hepatic veins	2.80 "

The average quantity of oxygen existing in venous blood generally is 8 per cent.; that is, it is reduced about one-half from its proportion in arterial blood.

Thus the blood-globules serve as carriers of oxygen from the lungs where it is absorbed, to the tissues where it is consumed; and the first object of respiration is to supply oxygen to the blood, in order that the blood may supply it to the tissues.

Exhalation of Carbonic Acid by the Blood.—The venous blood, as it returns to the right side of the heart, is already charged with carbonic acid to such an extent that a portion of this gas is exhaled through the pulmonary membrane, and discharged with the breath. Its absolute quantity in the blood has not been determined with the same accuracy as that of the oxygen. Carbonic oxide, which is so efficient for the extraction of oxygen from the blood, displaces only a portion of its carbonic acid; and in the experiments of Bernard, the maximum quantity of carbonic acid obtained from venous blood by this means was only about 6.5 per cent. by volume. A much larger proportion may be extracted by the mercurial air-pump, amounting on the average, in the experiments of Ludwig, to about 28 per cent. for arterial blood, and about 31 per cent. for venous blood. But a large part of the carbonic acid obtainable in this way does not exist in a free form in the blood, but in a state of combination with the alkaline phosphates and carbonates of the plasma; since it is known that a watery solution of sodium bicarbonate will lose a portion of its carbonic acid, and become reduced to the condition of a carbonate by being subjected to the influence of a vacuum, or even by agitation with pure hydrogen at the temperature of the body. Lehmann found[2] that after the expulsion from ox's blood of all the carbonic acid removable by the air-pump and a current of hydrogen, there still remained 0.1628 per cent. of sodium carbonate, with which a certain quantity of the carbonic acid previously given off must have been united in the form of bicarbonate.

It is estimated by Bert, according to the experiments of Fernet, that a portion of the carbonic acid of the blood is in simple solution and a

[1] Liquides de l'Organisme. Paris, 1859, tome i. p. 394.

[2] Physiological Chemistry, Cavendish edition. London, 1854, vol. i. p. 438.

portion combined with the alkaline salts; the blood, when artificially saturated with this gas, containing about three-fifths in a state of solution and about two-fifths in a state of combination. We do not know, however, what this proportion is in the venous blood as it exists in the living body; and the large amount of carbonic acid removable by the action of a vacuum does not represent that which is capable of being exhaled from the blood through the pulmonary membrane. This quantity is very much smaller. We know that, on the average, 13 cubic centimetres of carbonic acid are discharged from the lungs in man with each expiration; and during this interval, judging from the capacity of the left auricle and the frequency of its pulsations, there can hardly be less than 400 cubic centimetres of blood passing through the pulmonary circulation. This would give only a little over 3 per cent. as the volume of carbonic acid discharged from a given quantity of blood in respiration. The average results obtained by extraction with the mercurial air-pump, in the experiments of Ludwig, give this quantity as the actual difference between venous and arterial blood, as follows:

Average Quantity of Carbonic Acid removable by the Air-Pump, from

Venous blood	31.27 per cent.
Arterial blood	27.99 "
Difference	3.28 "

All the different modes of analysis, whether by carbonic oxide, other indifferent gases, or the air-pump, though differing in the quantity of gas extracted, show that there is less carbonic acid in arterial than in venous blood, and accordingly that this gas is exhaled from the circulating fluid during its passage through the lungs.

Unlike the oxygen, the carbonic acid of the blood is *principally contained in the plasma*, and not in the blood globules; since the capacity of absorption for this gas is not essentially different for the serum and for the entire blood.

Source of the Carbonic Acid of the Blood.—The source of the carbonic acid of the blood, as well as the destination of its oxygen, is in the tissues themselves. From the experiments of various observers it is found that every organized tissue, in the recent condition, has the power of absorbing oxygen and exhaling carbonic acid. G. Liebig, for example, showed that frogs' muscles, recently prepared and completely freed from blood, will continue to absorb oxygen and discharge carbonic acid. Similar experiments with other tissues have led to the same result. It is in the substance of the tissues, accordingly, that the oxygen becomes fixed and assimilated, and that the carbonic acid takes its origin. These two phenomena, however, are not immediately dependent upon each other. This is shown by the fact that animals and fresh animal tissues will continue to exhale carbonic acid in an atmosphere of hydrogen or of nitrogen, or even when placed in a vacuum. Marchand found that frogs would live for from half an hour to an hour

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in pure hydrogen gas; and that during this time they exhaled even more carbonic acid than in atmospheric air, owing probably to the superior displacing power of hydrogen for carbonic acid. For while 1000 grammes' weight of frogs exhaled about 0.077 gramme of carbonic acid per hour in atmospheric air, they exhaled during the same time in pure hydrogen as much as 0.263 gramme. The same observer found that frogs would recover on the admission of air after remaining for about half an hour in a nearly complete vacuum; and that if they were killed by total abstraction of the air, 1000 grammes' weight of the animals were found to have eliminated 0.600 gramme of carbonic acid. Similar facts were previously observed by Spallanzani; and Paul Bert found that while a certain quantity of fresh muscular tissue, in atmospheric air, exhaled in a given time 30 cubic centimetres of carbonic acid, the same quantity, in pure hydrogen, exhaled 23 cubic centimetres during the same time. He even found that the exhalation of carbonic acid would continue to go on, in an atmosphere of nitrogen, from muscular tissue which had previously been subjected for a quarter of an hour to the action of a vacuum.[1]

It is furthermore evident that in this process of internal respiration by the tissues, as in the external phenomena of respiration by the lungs, the quantities of oxygen absorbed and of carbonic acid exhaled do not always bear the same relation to each other. This is shown by the experiments of Paul Bert on the gases absorbed and discharged by the different tissues of the dog in contact with atmospheric air, where in some instances the volume of carbonic acid produced was greater, and in others less than that of the oxygen consumed; the proportions of the two varying considerably in each case.

The following list gives the result of a series of these experiments:

QUANTITY OF O AND CO_2 ABSORBED AND EXHALED DURING 24 HOURS, IN CUBIC CENTIMETRES.

By 100 grammes of	Oxygen absorbed.	Carbonic acid exhaled.
Muscle	50.8	56.8
Brain	45.8	42.8
Kidneys	37.0	15.6
Spleen	27.3	15.4
Testicles	18.3	27.5
Pounded bones	17.2	8.1

The production of carbonic acid by the tissues is not, therefore, directly connected with the absorption of oxygen. The precise chemical action by which carbonic acid originates in the solid organs is unknown; but it is probably by some mode of decomposition in which a portion of the carbon and oxygen present in the tissues separate from their previous combinations in this form, while the remaining elements at the same time unite to produce other substances of different composition.

The process of respiration consists, accordingly, in an interchange of

[1] Leçons sur la Physiologie comparée de la Respiration. Paris, 1870, p. 49.

gases between the blood and the lungs. The blood coming to the lungs comparatively poor in oxygen and charged with carbonic acid, the former gas is absorbed from the air in the pulmonary vesicles, while the latter is discharged at the same time, to be exhaled with the breath. These changes, however, are neither of them complete, but only partial, both for the air and for the blood. The expired air is never deprived of the whole of its oxygen, and contains only about 4 per cent. of its volume of carbonic acid. On the other hand, the venous blood coming to the lungs still contains a moderate percentage of oxygen; and a certain quantity of carbonic acid is also present in arterial blood. It is only the proportion of these gases which is changed in respiration, the carbonic acid of the blood being diminished, and its oxygen increased, by its passage through the pulmonary circulation.

The office of the respiratory apparatus is therefore to afford ingress and egress to the two substances which enter and leave the body in the gaseous form. These two substances have no immediate relation with each other, excepting as to the organ by which they are absorbed and exhaled. They represent the beginning and the end of a series of internal combinations and decompositions, which are among the most essential of the changes contributing to the maintenance of life.

CHAPTER XIV.

ANIMAL HEAT.

One of the characteristic properties of living creatures is that of maintaining, more or less constantly, a standard temperature, notwithstanding the external changes of heat or cold to which they are subjected. If a bar of iron or a vessel of water be heated to a temperature above that of the external air, and then left to itself, it will at once begin to lose heat by radiation and conduction; and this loss of heat will continue until, after a certain time, the temperature of the heated body has been reduced to that of the surrounding atmosphere. It then remains stationary at this point, unless the atmosphere should become warmer or cooler; in which case a similar change takes place in the inorganic body, its temperature remaining constant or varying with that of the surrounding medium.

With man and many animals the case is strikingly different. If a thermometer be introduced into the stomach or rectum of a dog, or placed under the tongue of the human subject, it will indicate a temperature of from 37° to 38° (about 100° F.),[1] whether the surrounding atmosphere at the time be warm or cool. This internal temperature of the body is sensibly the same in summer and in winter. Although the external air may be at the freezing point, the internal parts of the body, in a condition of health, will indicate their usual standard of warmth when examined by the thermometer; and even in ordinary summer weather the temperature of the air is, for the most part, many degrees below that of the living body. As the body, however, by exposure to such an atmosphere must be constantly losing heat by radiation and conduction, like any inorganic mass, and yet maintains a standard temperature, it is plain that a certain amount of heat must be generated in its interior, sufficient to compensate for the external loss. The internal heat, so produced, is known by the name of *vital* or *animal heat.*

Thus it is by its own internal heat that the body is warmed. The clothing used by man, and the fur, wool, or feathers by which the bodies of animals are protected, have, of course, no warmth in themselves; they simply prevent the body from losing heat too rapidly and thus becoming cooled down below its normal standard. Even the furnaces and fires of a dwelling house only serve in a similar way to moderate the cooling influence of the air; for the atmosphere, even in

[1] To convert any given number of degrees of the Centigrade scale into the corresponding value for the Fahrenheit scale, multiply by 1.8 and add 32 to the product.

the warmest apartment, never rises to the heat of the living body, which is still the only source of its own vital temperature.

Differences of Temperature in Different Classes of Animals.—The intensity of the production of internal heat varies in different classes of animals. As a rule, it is most active in birds, whose temperature is in general 45°. In the mammalians it is 37° to 40°; in man about 37.5. As in these two classes the internal organs and the blood are nearly always much above the temperature of the air or of the surface of the skin, and accordingly feel warm to the touch, they are called the "warm-blooded animals." In reptiles and fish, on the other hand, the production of heat is much less rapid, and preponderates so little over that of the air or water which they inhabit, that no marked difference is perceptible on cursory examination; and as their internal organs have a lower temperature than our own integument, and consequently feel cool to the touch, they are called the "cold-blooded animals." This difference, however, is only one in degree and not in kind. Reptiles and fish also generate heat within their bodies, which may be measured by the thermometer. The temperature of frogs, serpents, tortoises, water-lizards, and fish has thus been found to be from 1.7° to 4.5° above that of the surrounding air or water.

In the invertebrate animals, as insects and the like, the heat produced is still less easily perceptible because, from the great extent of the surface presented by their bodies in proportion to their mass, the warmth is more rapidly dissipated. But when many of them are collected in a small air-space, or when they are in a state of activity, it is still distinguishable by thermometric measurement. The temperature of the butterfly after active motion has been found to be from 2.77° to 5° above that of the air; that of the humble-bee from 1.5° to 5.5° higher than the exterior. According to the experiments of Newport, the interior of a hive of bees may have a temperature of 9° when the external atmosphere is at 1.4°, even while the insects are quiet; but if they be excited to activity by tapping on the outside of the hive, it may rise to 38.8°. Thus, while the insects are at rest, the thermometer indicates a very moderate temperature; but if kept in rapid motion in a confined space, they may generate a sufficient amount of heat to produce a sensible elevation in the course of a few minutes.

The production of heat is not confined to animal organisms, but takes place also in vegetables. Here, however, it is still more rapidly dissipated than in insects, owing to the great extent of surface presented by the ramifications and foliage, and to the abundant evaporation of moisture from the leaves, by which the heat generated is in great measure consumed without becoming perceptible by the ordinary thermometer. If this loss of heat from the plant be diminished by keeping the air charged with watery vapor and thus preventing evaporation, the elevation of temperature becomes sensible and may be measured. Dutrochet[1] first demonstrated, by the use of the thermo-electric needle, that

[1] Annales des Sciences naturelles. Paris, 2me Série, tome xii. p. 277.

nearly all parts of a living plant, such as the green stems, the leaves, the buds, and even the roots and fruit, generate a certain amount of heat; the maximum temperature thus detected being about 0.28° above that of the surrounding atmosphere. Subsequent observations have shown that in certain periods of vegetative activity, as in the processes of germination and flowering, the development of heat is much more rapid. In the malting of barley, when a considerable quantity of the germinating grain is piled in a mass, its elevation of temperature may be readily distinguished, both by the hand and the thermometer. The most striking example of heat-production in flowers is presented by those of the Araceæ (Calla, Indian turnip, Sweet flag) at the time of fecundation,[1] which in warm weather may show a temperature of 4°, 5°, or even 10° above that of the surrounding air.

The generation of heat is accordingly a phenomenon common to all living organisms, whether animal or vegetable. When the mass of the organized body is large in proportion to its extent of surface, the heat thus produced is readily distinguishable both by the touch and by the thermometer. When rapidly dissipated by increased extent of surface, and especially by the evaporation of moisture, it is less easily detected, but it exists in each case. In birds and mammalians it is more active than in reptiles and fish; and even in different species of animals belonging to the same class, it is usually found that the normal temperature of the body, like the other physiological phenomena, differs slightly, according to the special organization of the animal and the general activity of its functions.

Quantity of Heat in the Living Body.—The quantity of heat produced in the body within a given time is best measured by the increase of temperature which it will produce in a certain volume of water. Prof. John C. Draper[2] found that the human body, having a volume of about 85 litres (3 cubic feet) and a weight of 81.65 kilogrammes (180 pounds avoirdupois), by remaining at rest in the bath for one hour, could raise the temperature of 212 kilogrammes of water 1.11°; which he estimates, assuming the specific heat of the body to be about the same with that of water, would be capable of warming the body itself 2.77°. But as the temperature of the body, in the observation quoted, was lowered 0.55° while in the bath, the heat actually generated would be capable of warming the body itself, or an equal volume of water, 2.22°. This would be equivalent to 188.7 heat units,[3] produced by the human body in the course of one hour, or 2.31 heat units for every kilogramme of bodily weight.

The experiments of Senator[4] on the heat-producing power in dogs

[1] Sachs, Traité de Botanique. Paris, 1874, p. 847.

[2] American Journal of Science and Arts. New Haven, 1872, vol. ii. p. 445.

[3] A *heat unit* is the quantity of heat required to raise the temperature of one kilogramme of water from 0° to 1° of the centigrade scale.

[4] Archiv für Anatomie, Physiologie, und Wissenschaftliche Medicin. Leipzig, 1872.

were performed with much accuracy. The animals were inclosed in a copper cage, through which ventilation was kept up at a known rate, the temperature of the incoming and outgoing volumes of air being noted at intervals of ten minutes. The cage containing the animal was surrounded by a known volume of water, at from 26.5° to 29°, and the whole apparatus inclosed in an outer case made as nonconducting as possible; the quantity of heat actually lost from it by external cooling being determined by preliminary observations. The internal temperature of the animal having been taken, he was introduced into the cage and allowed to remain there a certain time. The heat produced within this time was mainly ascertained by the increase of temperature in the water surrounding the cage, the result being corrected by that of the air used for ventilation, as well as by the variation in temperature of the animal himself, and the loss from the apparatus by external cooling. By this method the experimenter found, as the average result of five observations, that a dog of 5.392 kilogrammes' weight, at rest and in the fasting condition, produced in one hour 12.63 heat units; that is, 2.34 heat units for every kilogramme of bodily weight. According to these experiments, the heat-producing power in the dog and that in the human subject are nearly the same; while that of the dog is rather the more active of the two.

Normal Variations of Temperature in the Living Body.—The temperature of the body is not the same in its different regions, but increases for a certain distance, from the exterior toward the central parts. This is because the living body is subjected to a constant loss of heat from the surface, like any other solid substance of higher temperature than the surrounding air. Consequently the integument and the parts immediately subjacent to it, being more exposed to this cooling influence than the internal organs, have habitually a temperature slightly below that of the body in general. Accordingly, whenever the external air rises to the neighborhood of 37° or 37.5° it feels uncomfortably warm; because, although this is exactly the normal temperature of the blood and the internal organs, it is considerably above that of the skin, which is readily sensitive to variations of cold or warmth. The cooling influence of the external atmosphere upon the skin is considerably moderated by the movement of the circulation; since the warmer blood coming from the internal parts constantly supplies the integument with fresh quantities of heat and thus tends to compensate for its external loss.

Notwithstanding this compensation, however, the difference in temperature between the external and internal parts of the body is always perceptible during health. If the bulb of a thermometer be held for some minutes between the folds of skin in the palm of the hand, it will stand at 36.4°; in the axilla, at 36.6°; under the tongue, it will reach 37.2°; in the rectum, 37.5°; and Dr. Beaumont found, in the case of Alexis St. Martin, that the thermometer, introduced into the stomach through the gastric fistula, often indicated a temperature of 37.8°. It is evident therefore that, in order to ascertain the real internal tempera-

ture of the body, the bulb of the thermometer should be inserted so deeply as to pass beyond the superficial zone affected by the process of external cooling. Even when placed beneath the tongue it is in contact with parts which are themselves slightly cooled by the passage of the air in inspiration and expiration, and accordingly does not reach the maximum temperature of the body. To accomplish this, it must be inserted into the abdominal cavity or the rectum, so deeply that a further introduction produces no increase in the indicated temperature. This is the method usually adopted in physiological observations.

Beside the differences observable from the above cause between the superficial and the deep-seated parts, there is a real variation within narrow limits of the internal temperature of the body, according to different physiological conditions. Jürgensen has shown[1] that in the human subject there is a *diurnal* variation, the temperature during the day being a little higher than at night, even when both periods are passed in complete repose. A series of observations upon the same individual in a state of rest gave the following averages:

Temperature of the Human Body when at rest.

By day.	By night.
37.34°	36.91°

The difference between the two averages amounts to 0.43°. There are also temporary variations of small extent during each of the above periods; the greatest variation during the day being 0.27°; that during the night 0.15°.

The temperature of the body is also increased by *muscular activity.* It is a matter of common observation, both in man and animals, that temporary exertion produces an increase of bodily warmth. Jürgensen observed in the same individual that while during a day of absolute rest the maximum temperature attained was 37.7°, under the influence of exercise it reached 38.8°. A much more striking difference, corresponding with muscular repose or activity, has already been mentioned as observable in insects.

The animal temperature is furthermore increased or diminished by a condition of *digestion or abstinence.* This was indicated in several instances by the observations of Jürgensen upon man, but is shown in a very marked degree by those of Senator upon the dog, in which the average production of heat was sensibly diminished by continued fasting and increased by the digestion of food. The following table shows the quantity of heat produced by the same animal, in the conditions of abstinence and digestion.

Quantity of Heat produced by the Dog in one hour.

After two days' fasting	10.90	heat units.
After one day's fasting	12.63	"
Fed one hour previously	18.87	"

[1] Die Körperwärme des gesunden Menschen. Leipzig, 1873.

As the production of heat in the body can only take place by the consumption or change of combination of its ingredients, it is evident that in continued abstinence from food, the materials susceptible of this change must be constantly diminishing in quantity; and the animal temperature accordingly, like other vital phenomena, becomes depressed from a deficiency in the sources of its supply.

Mode of Production of Animal Heat.

In all instances, so far as observation has gone, the production of heat in living organisms is in proportion to the activity of the internal changes going on in the body. These changes are more especially and constantly indicated by the absorption of oxygen and the exhalation of carbonic acid in respiration. Even in the vegetable kingdom, it is demonstrated by the researches of physiological botanists that the absorption of oxygen in plants is always accompanied both by the production of carbonic acid and by the evolution of heat; and the quantity of heat produced is greatest at the time when those processes are going on which, like germination and flowering, are accompanied by the most active absorption and exhalation of oxygen and carbonic acid respectively.

The same thing is manifest in the different classes of the animal kingdom. Birds and mammalians, where respiration is most active, have also the highest temperature; while in reptiles and fish the respiratory process is more sluggish, and the production of heat at the same time less abundant. A very close connection between the two phenomena is observable in hibernating animals, in which, during the winter sleep, respiration becomes comparatively inactive and the bodily temperature is also reduced to a very low standard. In the observations of Horvath[1] on the respiration of marmots, he found that these animals during cold weather are plunged in a profound stupor in which the movements of respiration are exceedingly infrequent and sometimes hardly perceptible. At certain intervals the animals awake for a short time, after which they again return to the state of insensibility. Horvath found that the internal temperature of the marmot, when awake, was from 35° to 37°; while, in the hibernating condition, it was reduced to 10°, 9°, or even to 2°, according to that of the surrounding air. On awakening, the temperature of the body rapidly rises. In one animal, the internal temperature during sleep was from 9° to 10°; but on awakening it rose at the end of an hour to 12°, in two hours to 17°, and in two hours and a half to 32°. Respiration also becomes increased in activity to a similar degree. A marmot weighing 153 grammes produced, while in the comatose condition, 0.015 gramme of carbonic acid per hour; and two days afterward, when awake, produced 0.513 gramme in the same time, that is, more than thirty times as much as when in the state of hibernation.

[1] Revue des Sciences Médicales. Paris, 1873, tome i. p. 59.

These and similar facts point to so close a relation between the intensity of respiration and that of heat-production, that the one of these processes may be taken, in general terms, as the measure of the other; particularly as respiration consists in the absorption of oxygen and the exhalation of carbonic acid, and as we know that the oxidation of carbonaceous matters, outside the body, is one of the readiest means for the production of heat.

This connection, however, is not an immediate one, nor can we consider the production of heat in the living body as a result of simple oxidation. We have already seen in the preceding chapter that the formation of carbonic acid is not due to direct oxidation, since it will go on in the tissues without the immediate presence of oxygen. Respiration is essential to *all* the phenomena of animal life, and may be taken as the criterion of vital activity in general. The production of heat is one of these phenomena, and, like the rest, increases or diminishes in intensity with that of respiration; but it cannot be said to depend upon respiration in any peculiar or exclusive manner.

The Evolution of Heat and the Products of Respiration not strictly proportional. — Furthermore, notwithstanding the general relation in activity between the two functions, if an accurate comparison be made between the quantity of heat produced, under different circumstances, and that of oxygen absorbed or of carbonic acid exhaled, they are found not to correspond exactly with each other. In the experiments of Senator on the bodily temperature in dogs, it was shown that the evolution of heat and the production of carbonic acid do not follow the same rate of increase. They are both augmented during digestion, but the production of carbonic acid never in the same degree with that of heat. An examination of the averages obtained in three series of observations gives the following result:

Quantities of Heat and of Carbonic Acid produced by the Dog in one hour.

	Condition of the animal.	Carbonic acid in grammes.	Heat units.	Proportion between the two.
Dog No. 1	Fasting	3.455	12.630	1 to 3.65
	In digestion . . .	5.013	18.875	1 to 3.76
Dog No. 2	Fasting	4.405	16.500	1 to 3.72
	In digestion . . .	4.837	19.390	1 to 4.01
Dog No. 3	Fasting	3.154	16.880	1 to 5.35
	In digestion . . .	3.846	21.960	1 to 5.71

Thus the proportion of carbonic acid formed to the heat produced is different in the three animals when compared with each other in the same condition; and it also varies in each animal under the different conditions of fasting and digestion.

In the experiments of the same observer on the effect exerted by artificial cooling on the animal body, he found that under the influence of a low temperature the actual production of heat in dogs was never increased, but was usually perceptibly diminished; while that of carbonic acid was generally somewhat increased and never diminished.

It is evident, accordingly, that the evolution of heat in the living animal is due to other causes than those which result in the immediate production of carbonic acid. Even outside the body a notable elevation of temperature may be produced by the hydration of quicklime, the mixture of alcohol and water, or of sulphuric acid and water, as well as other chemical or physical actions in which direct oxidation does not take part. Many analogous changes may take place in the process of internal nutrition, from which a part, at least, of the animal heat originates in the living body.

Local Production of Heat in the Organs and Tissues.—Although the living body, as a whole, presents a certain standard temperature, the production of heat takes place separately in each organ and tissue by the changes of nutrition which go on in its substance. This is shown by the fact that each separate organ has a special temperature of its own, which increases or diminishes according to its condition of activity or repose. A very considerable quantity of heat is thus produced in the substance of the *muscles.* The experiments of Becquerel and Breschet on the brachialis, in man, showed the temperature of this muscle in repose to be 36.5°; while, after repeated and energetic flexion, it was from 37° to 37.5°. Bernard,[1] by placing thermo-electric needles in the two gastrocnemii muscles of the dog, after section of the spinal cord to prevent voluntary movements, found the temperature of the muscles on the two sides to be sensibly equal; but on producing contraction by galvanizing one of the sciatic nerves, the temperature of the muscle on that side rose from 0.1° to 0.2°, at the same time that the venous blood of the muscle became darker in hue. Since the muscles constitute so large a part of the mass of the body, it is easy to understand how continuous muscular exertion should, after a time, produce a general elevation of temperature. In the muscles, during contraction, the increase in warmth is always accompanied by a greater consumption of oxygen, and consequently by a darker color of the venous blood.

Heat is also produced in the *glandular organs* when in active secretion, as shown by comparing the temperature of the arterial blood entering with that of the venous blood leaving the glandular tissue. Under these circumstances the venous blood coming from the gland is warmer than the arterial blood with which it is supplied. According to the observations of Bernard upon the submaxillary gland of the dog, while the gland is in repose, the circulation through its tissue is slow, its venous blood scanty and very dark-colored, and the oxygen of the arterial blood is reduced, in traversing the organ, to 40 per cent. of its original quantity; but when the gland is excited to active secretion, its circulation is increased in rapidity, its venous blood is more abundant and of a brighter color, its oxygen being only reduced to 61 per cent. of that contained in the arteries. At the same time its temperature

[1] Revue Scientifique. Paris, 1871, No. I., p. 1064.

rises, notwithstanding the consumption of oxygen is less than in the condition of glandular repose.

A similar elevation of temperature is shown by the blood while traversing the capillary circulation of the intestine and of the liver. The following tables give the results of two series of observations by Bernard on the temperature of the blood entering and leaving these two organs in the dog:

TEMPERATURE OF THE BLOOD IN THE

Aorta.	Portal Vein.
36.8°	38.8°
40.3°	40.7°
39.4°	39.5°

Portal Vein.	Hepatic Vein.
40.2°	40.6°
40.6°	40.9°
40.7°	40.9°

Thus the blood of the hepatic vein, after traversing two successive capillary circulations, is warmer than that drawn from any other part of the body.

Even in the kidneys, when the secretion of urine is actively going on, there is a rise of temperature in the blood of the renal veins. At the same time, as in the submaxillary glands, the circulation is increased in activity, the venous blood leaves the organ of a bright red color, and its proportion of oxygen, according to Bernard, is only reduced to 88 per cent. of that contained in the arteries, while in the condition of glandular repose it is reduced to 33 per cent.

The production of heat, therefore, is accomplished in the different organs of the body with different degrees of intensity according to the special nature of the act of nutrition in each one. In the muscles it is accompanied by an increased consumption of oxygen and a deeper coloration of the venous blood; in the salivary glands and the kidneys by a diminished consumption of oxygen and a less complete change in the color of the blood. The blood coming from each organ has a higher temperature in proportion to the activity of heat-production in the organ itself; and thus the temperature of the venous blood varies in different parts of the circulatory system, while that of the arterial blood is everywhere sensibly the same.

Cooling of the Blood in its Passage through the Lungs and Skin.—While in the other internal organs the blood is warmed during its passage through the capillary vessels, in the lungs its temperature is slightly diminished. This fact, which has been alternately asserted and denied, owing to the difficulties of exact observation without introducing other causes of a change of temperature, has been abundantly confirmed by the more recent observations of Hering, Bernard, Heidenhain and Körner, and Stricker and Albert. That of Hering was made upon a young calf, otherwise in good condition, but presenting the malformation of ectopia

cordis, by which the heart was withdrawn from the immediate contact of other organs, and in which case the blood of the right ventricle had a temperature of 39.37°, that of the left ventricle 38.75°. Heidenhain and Körner,[1] in 94 observations on the dog, partly with the use of thermo-electric needles and partly with the mercurial thermometer, found the temperature of the blood on the two sides of the heart equal in only one instance. In all the others, it was higher on the right side than on the left, by 0.1° to 0.6°. Bernard,[2] who first demonstrated this difference by the mercurial thermometer, has shown it also by the use of thermo-electric needles, introduced into the right and left ventricles of the dog's heart, through the jugular vein and carotid artery respectively; always finding the blood in the right ventricle warmer than that in the left. According to these observations, the difference in temperature may amount in the fasting animal to 0.174°, during digestion to 0.232°. Although during digestion the temperature of the blood generally is higher than in the fasting condition, the difference between the two sides of the heart continues to show itself in the same direction.

The diminution in temperature of the blood while passing through the lungs is usually attributed to the physical influence of the cooler air in the pulmonary cavities and to that of the vaporization of watery fluid. As the air expelled by respiration is warmer than when introduced into the lungs, it must withdraw a certain amount of heat from the internal parts; and as it contains, furthermore, watery vapor disengaged from the lungs, the vaporization of this fluid must also reduce the temperature of the respiratory organs. Whether the cooling influence of these causes is more or less than sufficient to account fully for the difference in the blood on the two sides of the heart has not been determined. It is possible that heat is also produced in the lungs, as in the other internal organs; but that the whole of it, and a little more, is consumed by the influence of the air upon the pulmonary membrane. It is evident, however, that physical conditions exist in the lungs which must cause the disappearance of more or less sensible heat; and it is certain that the blood, in point of fact, diminishes slightly in temperature while passing through the pulmonary circulation.

In the cutaneous circulation the same physical causes exist for a cooling effect on the blood as in the lungs; namely, the contact of the skin with the cooler air, and the vaporization of the watery fluid supplied by perspiration. It is for this reason, as already mentioned, that the superficial parts of the body have a normal temperature somewhat below that of the interior; and accordingly the blood, after passing through the vessels of the integument, returns to the centre with its temperature slightly diminished. There is every reason to believe that the tissues of the skin and subjacent parts evolve a certain amount of heat by their own nutritive changes; but the heat thus produced, as in the case of the

[1] Archiv für die Gesammte Physiologie. Bonn, 1871, Band iv. p. 558.

[2] Revue Scientifique. Paris, 1871, No. 1, p. 946.

lungs, being rather more than counterbalanced by that lost from the surface, the total effect upon the circulating fluid is a lowering of its temperature. The amount of warmth thus lost will vary with the degree of external cold and other conditions of the atmosphere which influence the rapidity of the abstraction of heat.

Local Elevation of Temperature by increased Circulation.—If the circulation be increased in any part of the external integument, the immediate effect produced is a local rise of temperature. This was first shown by Bernard in his experiments upon division of the sympathetic nerve on one side of the neck. If this operation be performed upon the rabbit, the consequence is a relaxation of the bloodvessels in the corresponding side of the head, an increased vascularity of the parts, most readily seen in the semi-transparent tissues of the ear, and a higher temperature, readily perceptible both by the touch and the thermometer. In a rabbit, after section of the sympathetic nerve upon the right side of the neck, the temperature of the corresponding ear, as indicated by the thermometer, was increased from 25° to 32°; and the difference between the two sides is usually more marked as the external air is colder. Since the superficial parts of the body are habitually cooler than the internal on account of their exposure to the air, and as they are constantly supplied with warm blood from the interior, their actual temperature will be increased in proportion to the amount of blood circulating through their vessels. The local rise of temperature in these instances is a passive one, the exposed tissues being warmed at the expense of the blood coming from the internal organs. No more heat is actually produced in the body than usual, and the cooling effect of the air upon the whole system is unchanged; but it is less perceptible in the part subjected to experiment, because it receives a larger quantity of heat from the interior owing to the increased volume of blood passing through it in a given time.

This influence of the circulation upon the temperature of the external parts has been shown by Dr. Wier Mitchell[1] by observations upon the human subject. If the hand and arm be held for some moments above the head, emptied as fully as possible of blood, and a tourniquet then applied to the arm in such a way as to check the circulation, the temperature of the hand falls 0.55°. If, on the contrary, the circulation be left unimpeded, and a freezing mixture applied to the elbow, sufficient to chill the ulnar nerve, when sensation has become entirely abolished the temperature of the corresponding hand rises from 1.10° to 2.20°. But if the arm be first emptied of blood as before, the tourniquet applied, and the ulnar nerve then chilled to insensibility, the temperature of the hand no longer rises, but falls, as in the former experiment, 0.55°.

In the internal or glandular organs, on the other hand, when excited to functional activity, the rise of temperature is an active one, taking place in the substance of the gland itself; since the blood

[1] Archives of Scientific and Practical Medicine. New York, 1873, vol. i. p. 354.

passing through these organs becomes warmer instead of cooler, and receives heat from the changes taking place in the glandular tissue.

Equalization of Temperature by the Circulation.—As the production of heat is a local process in each separate organ or tissue, varying in intensity with the nature of the nutritive changes in different parts, the blood, as we have seen, acquires a higher temperature in some organs than in others; and in the lungs and skin its heat actually diminishes instead of increasing. If it remained at rest, these differences of temperature would no doubt be more marked than they are at present. But as the blood is in constant motion, passing from the circumference to the centre, and being again distributed from the centre to the circumference, the effect of this movement of circulation is to equalize to a considerable degree the temperature of different parts of the body. The venous blood coming from the general integument with a diminished temperature is mingled with that of the muscular system, which has become warmed during its capillary circulation. The blood of the hepatic veins, which is the warmest of all, joins the current of the inferior vena cava, returning from the pelvic organs and the inferior extremities. This is again mingled, at its entrance into the right cavities of the heart, with the slightly cooler column of blood descending from the head and upper extremities by the superior vena cava. The whole volume of the blood then passes through the lungs, with the effect of still further moderating its temperature; and the arterial blood is then distributed to the various parts of the body, to gain warmth in some of them and to lose it in others, and again mingled after a few seconds at the centre of the circulation. Thus the superabundant heat of certain organs, where its production is most active, is constantly transferred to others by the moving column of the blood; and a certain equilibrium or standard of temperature is thus established for the body as a whole. It is found, by the observations of Jürgensen, that this standard temperature for the human body, as measured in the rectum, varies within very narrow limits, from day to night, and even at successive periods of each division of the twenty-four hours. These normal fluctuations are no doubt owing to the greater or less activity, at different times, of different internal organs; the total amount of heat produced being increased or diminished with the preponderating influence of organs in which it is more or less rapidly generated.

Regulation of the Animal Temperature.

A certain temperature is not only the result of the vital actions; it is also necessary to their accomplishment. Even in the vegetable kingdom this temperature, which varies within moderate limits in different kinds of plants, is requisite for all the phenomena of growth and vitality. A seed sown in the most productive soil does not germinate until it feels the influence of the necessary warmth; and its germination is also impossible if it be exposed to a heat which is too intense. The degrees both of heat and cold which favor or arrest the functions of vegetation

have been in many instances accurately determined. According to the experiments of Sachs, the limits of germination for wheat and barley are between 5° and 38°, and for Indian corn between 9° and 42°. The irritability and periodic movements of the sensitive-plant do not show themselves unless the temperature of the surrounding air be above 15°. In air at 48° to 50°, on the other hand, the leaflets become rigid in a few moments, though they may afterward recover if the temperature be moderated; while a heat of 52° permanently destroys their vitality. Thus no vegetative function can come into activity, unless the temperature of the plant reaches a certain degree above the freezing point; and it ceases, furthermore, if the temperature rise above another determinate degree, which cannot for any considerable time exceed 50°. Within these two limits, also, every vegetable function has a special temperature at which it is most active; diminishing in intensity both above and below this point.

Observation shows that the same is true of the animal functions. Each species of animal has a definite bodily temperature, and this temperature cannot be raised or lowered beyond certain limits without arresting the phenomena of life. Mammalians, whose normal temperature is from 37° to 40°, become insensible and soon die, when cooled down to 18° or 20°, which is the natural standard for reptiles and fish; while a frog is soon killed by being kept in water at 38°. On the other hand, mammalians die when their blood and internal organs are heated up to 45°, which is precisely the normal temperature of birds; and birds themselves are fatally affected when their internal temperature is raised to 48° or 50°. In every case the vital functions are seriously disturbed by a very moderate change in the actual temperature of the bodily organs; and in the mammalians, as a general rule, death follows when this change amounts to an elevation of 6° or 7°, or to a depression of 20°.

In the human subject, in febrile affections, the rise of temperature, as measured in the axilla, yields a very accurate criterion of the gravity of the disease. An increase of this temperature from 36.6° to 37.5° or 38° indicates a mild form of the malady; but an increase to 40° or 40.5° shows that the attack is severe. Above 40.5° it is a symptom of great danger; and when the temperature rises to 42.5° or 43° a fatal result is almost inevitable.[1]

Effects of Lowering the Temperature of the Animal Body.—If a warm-blooded animal be exposed to cold in such a way as to abstract the internal heat faster than it can be produced, the effect is a general and continuous depression of the vital functions. After a short period of pain in the more exposed and sensitive parts, the skin becomes insensible, the muscles lose their contractile energy, the movements of respiration diminish in frequency, and the nervous system becomes more and more inactive. In the human subject a marked sluggishness of

[1] Flint, Principles and Practice of Medicine. Philadelphia, 1868, p. 109.

mind and a disposition to sleep have been observed as among the symptoms of long continued and dangerous exposure to unusually low temperatures.

The local effects of cold upon the nervous tissues in man have been shown by the experiments of Dr. Weir Mitchell,[1] in chilling the ulnar nerve at the elbow by the application of a freezing mixture. This at first produces pain in the hand, subsequently followed by loss of sensibility and motive power in the parts corresponding with the distribution of the nerve.

The general effects of a lowered temperature result from its combined influence upon all the separate organs and tissues. According to the observations of Bernard, if the body of a rabbit or a guinea-pig be surrounded by snow or ice so as to prevent spontaneous motion and to cause a continuous abstraction of heat, the temperature, as taken in the rectum, gradually falls from 38° to 30°, 25°, 20°, and 18°. When the depression of the bodily temperature has reached this point, the animal is insensible and paralyzed, and the respiration feeble and infrequent. The heat-producing power is also lost, so that if the animal be withdrawn from the cooling mixture and kept in the air at 10° or 12°, the temperature of the body continues steadily to diminish, and death takes place after a short time.

But when in this condition of depression and insensibility, although most of the vital actions are suspended, and the animal has lost the power of maintaining his own temperature, if he be supplied with artificial warmth up to a certain point, he may regain his vitality, and the processes of life be again put in operation. The respiration, which was reduced to a minimum by the continued action of cold, becomes increased in rapidity as the body is artificially warmed, and the functions of the nervous and muscular systems are also finally restored.

A striking example of the temporary suspension of the bodily functions by cold is presented by the *hibernating animals*, as marmots and some species of squirrels, which pass into a condition of torpor during the winter, becoming insensible, unconscious, and immovable, while at the same time respiration is nearly imperceptible, and the bodily temperature sinks to 10°, 8°, or even 2°. Life, however, is not abolished but only held in abeyance; and with the return of spring all the functions resume their activity. A hibernating animal is accordingly somewhat in the condition of a seed, which remains in the ground over winter, with its vitality dormant, but ready to come into action when supplied with the requisite degree of warmth.

Effects of Elevating the Temperature of the Animal Body.—If the temperature of the body, in a living animal, be artificially raised some degrees above the normal standard, the effects are quite different from those produced by cold. In the experiments of Bernard, the animals, both birds and mammalians, were inclosed in a cage with heated air;

[1] Injuries of Nerves and their Consequences. Philadelphia, 1872, p. 59.

the air being sometimes dry and sometimes loaded with moisture, but renewed by due ventilation. The primary effects were increased frequency of respiration and an appearance of discomfort and agitation; and finally death took place usually with convulsive movements, sometimes accompanied by an audible cry. The fatal result was more rapidly produced in birds than in mammalia. Thus, a rabbit placed in the cage with dry air at 65°, died in twenty minutes; and a bird, in air at the same temperature, died in four minutes. This difference is no doubt partly due to the greater activity of the circulation in birds, by which external heat is more rapidly transferred to the internal organs; since the same observer found that of two rabbits, one living and one dead, placed in the warm cage at 100°, the internal temperature of the living animal became sensibly raised sooner than that of the dead one. In a medium of high temperature, therefore, a fatal amount of heat reaches the internal organs more rapidly by means of the circulation than by simple conduction through the solid tissues.

After death from exposure to too warm an atmosphere, the internal temperature is found to be 5° or 6° above the normal standard; the heart is motionless; both the muscles and the nerves are insensible to the stimulus of galvanism; and lastly, cadaveric rigidity is established with unusual promptitude. In many instances the blood is found dark-colored in the arterial as well as in the venous system; but this is a post-mortem change, since observation shows that the arterial blood continues red so long as life lasts, while its oxygen disappears and its color darkens with great rapidity after the stoppage of respiration. The appearances indicate that an unnaturally high temperature produces death by hastening, in an undue degree, the chemical changes taking place in the tissues and fluids, in such a manner that their vitality is rapidly exhausted and can no longer be maintained by the usual processes of nutrition.

Resistance of the Living Body to Low External Temperature.—Since an actual depression of the temperature of the body is followed by such serious results, and as, in point of fact, its temperature is maintained in health at the normal standard, notwithstanding exposure to varying degrees of cold, it is evident that the living organism possesses the power of increased production of internal heat, to compensate for the greater loss without. In the experiments of Senator on the abstraction of warmth, by confining dogs in close cages surrounded by a cold medium, it was found that the total amount of heat produced by the animal was not increased. But in these cases the animals were placed under conditions by which their natural movements were prevented, and the results obtained were due to simple cooling of the body, without the action of compensating causes. In the natural, unconfined condition, the effect is different. It is a matter of common observation, that the influence of moderate external cold, if not too long continued, produces a sense of warmth and increased vigor, instead of depression. The atmosphere of a winter's day, or a cold shower bath, acts as a

stimulant to vital processes; and, even although the exposed parts of the skin may be reduced considerably below their normal temperature, the body, as a whole, does not experience a loss of warmth, but maintains its natural condition of vitality. It is certain that under these circumstances more heat than usual must be produced from the influence of external cold.

The mode in which this result is accomplished has not been determined with precision by experimental means. It is plain that the nervous system has its share in the mechanism of the process, perhaps by directly stimulating the molecular changes which produce the evolution of animal heat. There are, however, two sources of heat supply, which evidently play an important part in maintaining the temperature of the body when exposed to cold.

The first of these is *muscular activity.* It has been shown that the muscles produce a considerable quantity of heat in their own tissue, and that this quantity is increased by the contraction of the muscular fibres. The total production of heat, therefore, for the whole body, must be considerably augmented when all the voluntary muscles are thrown into a condition of unusual functional activity. Experience shows that this is, in fact, one of the requisite conditions of resistance to cold. The stimulus of the cool air upon the skin excites the desire for active movement, and muscular exercise produces a compensating quantity of internal heat. But if the body be exposed to even moderate winter weather without voluntary motion, it must either be protected by an unusual quantity of clothing, or it will soon feel the depressing effect of a loss of its animal heat.

Secondly, the increased production of warmth, when required, is provided for by an *increased supply of food.* The materials for the chemical changes requisite for heat-production are supplied directly by the tissues or the blood, but primarily, of course, from the ingredients of the food. Even a recent ingestion of food, as shown in the experiments of Senator, increases perceptibly the amount of heat generated, in the dog, within a given time; and for longer periods, the influence of an ample or a scanty supply is abundantly manifest. In animals which are scantily fed or ill nourished, the capacity for resistance to cold is much less than in those which are in good condition and which have received a sufficient quantity of food. The immediate effect of a moderate exposure to cold in the healthy condition, is to increase the appetite. A larger quantity of food is habitually taken during the winter than during the summer season; and among the inhabitants of northern and arctic regions, the daily consumption of food is much greater than in the temperate and tropical climates.

It is not necessary to assume that the food, thus required for maintaining a greater heat-production, is directly employed to furnish the necessary warmth by its consumption. The heat is no doubt generated from the activity of all the nutritive changes in the different tissues of the body, and these changes are enabled to continue indefinitely only by

a supply of food sufficiently ample to provide for the material demands of the animal system.

Resistance of the Living Body to High External Temperature.—It has been seen that, in the human subject and the warm-blooded animals generally, an actual rise in the bodily temperature of 6° or 7° is certainly fatal; and yet the body may be exposed, as shown by repeated observations, to much higher degrees of heat without any injurious result. According to Dr. Carpenter, the temperature of the air, in many parts of the tropical zone, often rises, during a large portion of the year, to 43.3°, and in some regions of India is occasionally above 50°; while it is well known that the air of manufactory drying-rooms and of the Turkish bath may be easily endured at a heat of considerably more than 45°. Either of these temperatures would be fatal to man, if they indicated the actual warmth of the internal organs. The body therefore must either possess some means of diminishing its own production of heat, or else of neutralizing, to a certain extent, temperatures which are higher than that of the normal standard.

The most direct and simplest means of moderating the temperature of the body is that by the *cutaneous perspiration.* This fluid, derived from the perspiratory glands of the skin, is a clear, colorless, watery secretion, with a distinctly acid reaction, and a specific gravity of 1003 or 1004. Its constitution is as follows:

COMPOSITION OF THE CUTANEOUS PERSPIRATION.

Water	995.50
Sodium chloride	2.23
Potassium chloride	0.24
Sodium and potassium sulphates	0.01
Salts of organic acids	2.02
	1000.00

It is accordingly a fluid of very simple composition, containing more than 99½ per cent. of water, and more than half its solid ingredients consisting of the inorganic alkaline chlorides. There are also present in the perspiration traces of an organic substance similar to albumen, and a free volatile acid, which gives to the fluid its acid reaction and odor.

The perspiration is a constant secretion. In a condition of repose or of moderate bodily activity, it is exuded in so gradual a manner that it is at once carried off by evaporation, and has received the name, under these circumstances, of the *insensible transpiration.* The entire quantity of fluid discharged in this way, according to the observations of Lavoisier and Seguin, amounts on the average to 900 grammes per day. In addition to this, about 500 grammes are discharged from the lungs, making 1400 grammes of daily exhalation from the whole body. The vaporization of this quantity of water will consume 750 heat units; or

about one-fifth of all the heat produced in the body during twenty-four hours.

The cutaneous secretion may be greatly increased by temporary causes. An elevated temperature or unusual muscular exertion, will increase the circulation through the skin and largely augment the amount of fluid discharged. It then exudes more rapidly than it can be carried off by evaporation, and collects upon the skin as a visible moisture, whence it is known as the *sensible* perspiration. The amount of perspiration discharged during violent exercise has been known to rise as high as 350 or 380 grammes per hour; and Dr. Southwood Smith[1] found that the laborers employed in heated gas-works sometimes lost, by both cutaneous and pulmonary exhalation, nearly 1600 grammes in the course of an hour. The evaporation of this increased quantity of fluid consumes a large portion of the caloric derived from the heated atmosphere, and thus prevents an undue rise in the temperature of the bodily organs.

It is possible that certain influences transmitted through the nerves may also have the power of controlling directly the molecular activity of the tissues, and may thus diminish the amount of internal heat at the source of its production; but the experimental evidence of this action is yet incomplete, and its mode of operation comparatively obscure.

The production of heat in the animal body and the regulation of its temperature, by which it is maintained at or near a normal standard, are two of the most important phenomena presented by the living organism. They are the result of an associated series of vital actions, and at the same time essential conditions for the continuance of life.

[1] Philosophy of Health. London, 1838, chap. xiii.

CHAPTER XV.

THE CIRCULATION.

THE blood is a nutritious fluid, holding in solution the ingredients necessary for the formation of the tissues. In all the higher animals and in man, the structure of the body is compound, consisting of various organs, with widely different functions, situated in different parts of the frame. In the intestine the process of digestion is accomplished, and the prepared ingredients of the food are thence absorbed into the blood-vessels, by which they are transported to distant parts. In the lungs the blood absorbs oxygen, which is afterward appropriated by the tissues; and the carbonic acid produced in the tissues is finally exhaled from the lungs. In the liver, the kidneys, and the skin, other substances are produced or eliminated, and these local processes are all necessary to the preservation of the general organization. The circulating fluid is therefore a *means of transportation*, by which substances produced in particular organs are dispersed throughout the body, or by which substances produced in the tissues generally are conveyed to particular organs, in order to be eliminated.

The circulatory apparatus consists of four different parts, namely, 1st. The heart; a hollow, muscular organ, which propels the blood. 2d. The arteries; a series of branching tubes, which convey it from the heart to different parts of the body. 3d. The capillaries; a network of inosculating tubules, interwoven with the substance of the tissues, which bring the blood into intimate contact with their component parts; and 4th. The veins; a set of converging vessels, destined to collect the blood from the capillaries, and return it to the heart. In each of these different parts of the circulatory apparatus, the movement of the blood is peculiar and dependent on special conditions.

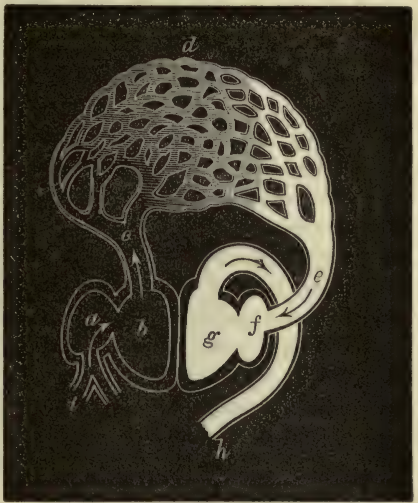
The Heart.

The structure of the heart and of the adjacent vessels varies in different classes of animals, owing to the different arrangement of the respiratory organs.

In man and the mammalians the process of respiration is not only much more active than in cold-blooded animals, but the lungs are also the only special organs of aeration. The whole of the blood, accordingly, after returning from the general system, passes through the lungs before it is again distributed to the system. It thus traverses in succession the general circulation for the whole body, and the special circulation for the lungs. The mammalian heart (Fig. 99), consists of

a right auricle and ventricle (a, b), receiving the blood from the vena cava (i), and driving it to the lungs; and a left auricle and ventricle (f, g) receiving the blood from the lungs and propelling it outward through the arterial system.

Fig. 99.



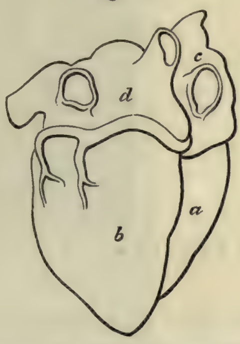
CIRCULATION IN MAMMALIANS.—*a.* Right auricle. *b.* Right ventricle. *c.* Pulmonary artery. *d.* Lungs. *e.* Pulmonary vein. *f.* Left auricle. *g.* Left ventricle. *h.* Aorta. *i.* Vena cava.

In the mammalian heart, the different parts of the organ present certain peculiarities and bear certain relations to each other, which influence its action and movements. The heart itself is suspended somewhat freely in the cavity of the chest, attached to the spinal column mainly by the great bloodvessels passing through the superior and posterior mediastinum. It is of a more or less conical form; its base, situated upon the median line, being directed upward and backward, while its apex points downward, forward, and to the left, surrounded by the pericardium, but capable of a certain degree of lateral and rotatory motion. The auricles, which have a smaller capacity and thinner walls than the ventricles, are situated at the upper and posterior part of the organ (Figs. 100 and 101); while the ventricles occupy its anterior and lower portions. The two ventricles, moreover, are not situated on the same plane. The right ventricle occupies

Fig. 100.

HUMAN HEART, anterior view.—*a.* Right ventricle. *b.* Left ventricle. *c.* Right auricle. *d.* Left auricle. *e.* Pulmonary artery, *f.* Aorta.

Fig. 101.



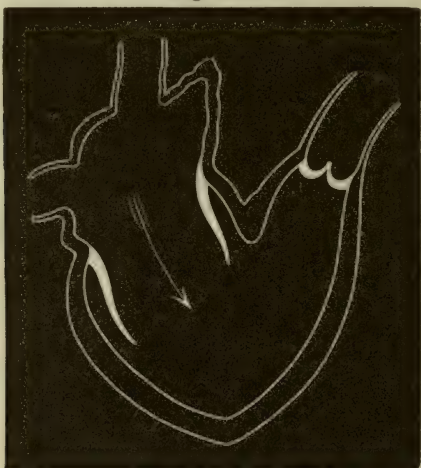
HUMAN HEART, posterior view.—*a.* Right ventricle. *b.* Left ventricle. *c.* Right auricle. *d.* Left auricle.

a position somewhat in front and above that of the left; so that in an anterior view of the heart the greater portion of the left ventricle is concealed by the right (Fig. 100), and in a posterior view the greater portion of the right ventricle is concealed by the left (Fig. 101); while in both positions the apex of the heart is constituted altogether by the point of the left ventricle.

The different cavities of the heart and of the adjacent bloodvessels on each side, though continuous with each other, are partially separated by certain constrictions. The orifices by which they communicate are known by the names of the auricular, auriculo-ventricular, and aortic and pulmonary orifices; the auricular orifices being the passages from the venæ cavæ and pulmonary veins into the right and left auricles; the auriculo-ventricular orifices leading from the auricles into the ventricles; and the aortic and pulmonary orifices leading from the ventricles into the aorta and pulmonary artery respectively.

The auriculo-ventricular, aortic, and pulmonary orifices are furnished with valves, which allow the blood to pass readily from the auricles to the ventricles, and from the ventricles to the arteries, but shut back in such a manner as to prevent its return in the opposite direction. The course of the blood through the heart is, therefore, as follows (Fig. 102):

Fig. 102.

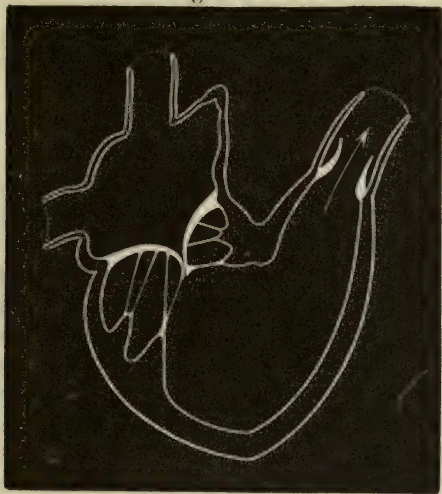


RIGHT AURICLE AND VENTRICLE; Auriculo-ventricular Valves open, Arterial Valves closed.

From the vena cava it passes into the right auricle; and from the right auricle into the right ventricle. On the contraction of the right ventricle, the tricuspid valves shut back, preventing its return into the auricle (Fig. 103); and it is thus driven through the pulmonary artery to the lungs. Returning from the lungs, it enters the left auricle, thence passes into the left ventricle, from which it is finally delivered into the aorta, and distributed throughout the body. The two streams of blood,

arterial and venous, in their passage through the heart, follow a course which is, in each case, curvilinear and more or less spiral in direction;

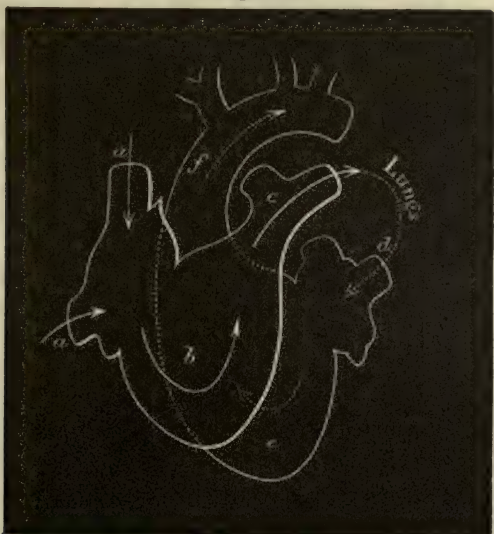
Fig. 103.



RIGHT AURICLE AND VENTRICLE; Auriculo-ventricular Valves closed, Arterial Valves open.

the axes of the currents crossing each other in the right and left cavities of the organ respectively (Fig. 104). The venous blood, received

Fig. 104.



COURSE OF BLOOD THROUGH THE HEART.—*a, a.* Vena cava, superior and inferior. *b.* Right ventricle. *c.* Pulmonary artery. *d.* Pulmonary vein. *e.* Left ventricle. *f.* Aorta.

by the right auricle from the two venæ cavæ, passes downward and forward from the auricle into the ventricle. In the body of the right

ventricle it turns upon itself and then follows a direction from below upward, from right to left and from before backward, through that part of the right ventricle lying in front of the heart and termed the "conus arteriosus," to the commencement of the pulmonary artery. On returning from the lungs to the left auricle, it passes from above downward into the cavity of the left ventricle, when it makes a turn like that upon the right side and is directed again from below upward and from left to right, behind the situation of the conus arteriosus, and crossing it at an acute angle, to the commencement of the aorta. The aorta itself, though its point of origin is placed somewhat posteriorly to that of the pulmonary artery, soon comes more to the front in its arched portion, while the pulmonary artery runs almost directly backward. Thus the two blood-currents may be said to twist spirally round each other in their course through the corresponding auricles and ventricles.

The movement of the blood through the cardiac cavities is not a continuous and steady flow, but is accomplished by alternate contractions and relaxations of the muscular walls of the heart; by which successive portions of blood are delivered from the auricles into the ventricles, and thence discharged into the arteries. Each one of these successive actions is called a beat or *pulsation* of the heart. The cardiac pulsations are accompanied by certain physical phenomena dependent upon the structure of the heart and its mode of action.

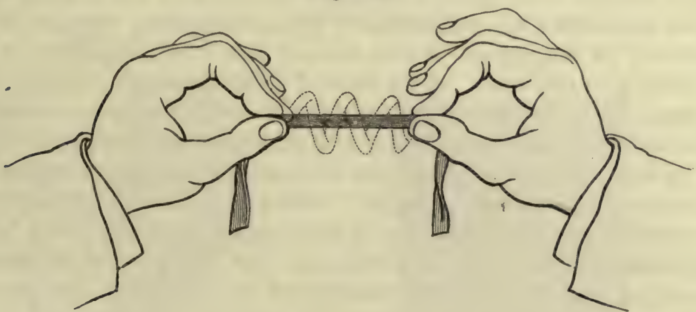
Sounds, Movements, and Impulse of the Heart.—The sounds of the heart are two in number. They can be heard by applying the ear over the cardiac region, when they are found to be quite different from each other in position, tone, and duration. They are distinguished as the *first* and *second* sounds of the heart. The first sound is heard with the greatest intensity over the anterior surface of the heart, and particularly at the situation of the apex beat, over the fifth rib and the fifth intercostal space. It is comparatively long, dull, and smothered in tone, and occupies one-half the entire duration of a beat. It corresponds in time with the impulse of the heart in the precordial region, and with the stroke of the large arteries in the immediate vicinity of the chest. The second sound follows almost immediately upon the first. It is heard most distinctly at the situation of the aortic and pulmonary valves, namely, over the sternum at the level of the third costal cartilage. It is short and distinct, and occupies only about one-quarter of the whole time of a pulsation. It is followed by an equal interval of silence; after which the first sound again recurs. The whole time of a cardiac pulsation may be divided into four quarters, of which the first two are occupied by the first sound, the third by the second sound, and the fourth by an interval of silence, as follows:

RELATIVE TIME AND DURATION OF THE HEART-SOUNDS.

Cardiac pulsation	1st quarter	First sound.
	2d "	
	3d "	Second sound.
	4th "	Interval of silence.

The cause of the *second* sound is universally admitted to be the sudden closure and tension of the aortic and pulmonary valves. This fact is established by the following proofs: 1st. The sound is heard with perfect distinctness, as mentioned above, directly over the situation of these valves at the base of the heart; 2d. The further we recede in any direction from this point, the fainter becomes the sound; and 3d, in experiments upon the living animal, by different observers, it has been found that if a curved needle be introduced into the base of the large vessels, so as to hook back the semilunar valves, the second sound disappears, and remains absent until the valve is again liberated. The valves consist of fibrous sheets, covered with a layer of endocardial epithelium. They have the form of semilunar festoons, the free edge of which is directed from the cavity of the ventricle, while the attached edge is fastened to the inner surface of the base of the artery. While the blood is passing from the ventricle to the artery, the valves are thrown forward and relaxed; but when the artery reacts upon its contents they shut back, and their fibres, becoming suddenly tense, yield a clear, characteristic, snapping sound. The character of this valvular sound may be closely imitated by snapping a piece of tape or ribbon (Fig. 105),

Fig. 105.



alternately loosening and extending it, while firmly held between the fingers of the two hands. A short piece of ribbon by this sudden tension will give out a sharp and distinct sound; a longer one will yield a sound which is more dull and prolonged.

The *first* sound of the heart contains two elements, which are mingled in different proportions according to the point at which it is heard. One of these elements is comparatively dull in tone, and when heard over the apex or front of the heart communicates its character to the whole of the first sound. It is variously attributed to the muscular contraction of the cardiac fibres and to the movement of the surface of the heart against the inner walls of the chest. The remaining element of the first sound is valvular in character, and is caused by the tension of the auriclo-ventricular valves at the time of the ventricular pulsation. It gradually predominates over the other, at points further removed from the apex of the heart, toward the left border of the organ and the

left nipple; and still further to the left it is heard alone, the first sound at this situation being purely valvular, like the second.[1]

The *movements* of the heart may be observed in the dog, or other warm-blooded quadruped, by opening the cavity of the chest by a longitudinal incision through the sternum, and separating the costal cartilages, on each side, at their junction with the ribs; artificial respiration being maintained by the nozzle of a bellows inserted in the trachea. The animal may be partially narcotized by a preliminary subcutaneous injection of morphine, after which complete etherization is produced and continued with great facility. The operation of opening the chest and exposing the thoracic organs increases the rapidity of the heart's movements and diminishes their force; but its action is not otherwise changed, and the circulation will continue for several hours, provided artificial respiration be maintained with regularity.

When exposed to view under these conditions, the movements of the mammalian heart are at once seen to be complicated to such a degree that close examination is requisite to distinguish their different elements. The most obvious appearance at first presented is the rapid succession of two alternating conditions, namely a condition of rest and a condition of movement. Furthermore, if the heart be touched or gently grasped between the fingers, it becomes evident that the two states of rest and movement are accompanied by corresponding changes in the consistency of the organ. At the time of rest it is comparatively soft and yielding to the touch; at the time of its movement, it becomes hard and tense. Inspection alone cannot determine which of these two states corresponds with the entrance of the blood into the ventricles and which with its exit; in other words, which represents muscular relaxation and which the contraction of the heart. Different observers, while watching the movements of the same heart in the living animal, will often be led to opposite conclusions in this respect. The only method of directly determining the point is that first adopted by Harvey, in his observations upon the heart, which formed the basis of the discovery of the circulation of the blood. If we insert through the walls of the left ventricle a silver canula from one to two millimetres in diameter, so as to pierce its cavity, the blood is forcibly projected from its orifice at the time of the tension of the cardiac walls, while its flow is suspended in the intervals of repose.

Thus the two states of relaxation and tension of the heart correspond with the relaxation and contraction of its muscular fibres. Like muscular tissue elsewhere, that of the heart during relaxation is comparatively soft to the touch; when the ventricles contract upon their contents and forcibly expel the blood, they become tense and firm, by the sudden rigidity of their fibres. By this means the two opposite conditions of the diastole and systole of the ventricles may be recognized with certainty, and connected with the other corresponding phenomena of the

[1] Flint, Treatise on Diseases of the Heart. Philadelphia, 1870, pp. 61–62.

heart's action. At the time of their diastole, the blood enters the cavity of the ventricles through the auricular orifice; at the time of their systole it is expelled into the arterial trunks.

Simultaneously with the hardening and contraction of the ventricles the apex of the heart moves slighly from left to right, and rotates at the same time upon its own axis in a similar direction. This movement was also observed by Harvey, who describes it as follows:[1]—

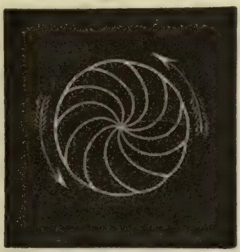
"And if any one," he says, "bearing these things in mind, will carefully watch the motions of the heart in the body of the living animal, he will perceive not only all the particulars I have mentioned, namely, the heart becoming erect and making one continuous motion with its auricles; but, further, a certain obscure undulation and lateral inclination in the direction of the axis of the right ventricle, the organ twisting itself slightly in performing its work."

Both these movements, of lateral inclination and rotation, result from the spiral arrangement of the muscular fibres on the exterior of the heart. The most superficial of these fibres start from the base of the organ and pass toward its apex, following an obliquely spiral course over its anterior surface, from above downward and from right to left. The contraction of this superficial portion of the muscular fibres accordingly tilts the apex of the heart in a slight degree bodily from left to right. As the fibres, however, reach the point of the heart they curl round its axis, change their direction, and disappear from sight, becoming deep seated and passing upward along the septum and internal surface of the ventricle, to a termination finally in the columnæ carneæ and the fibrous border of the auriculo-ventricular ring. They thus form, exactly at the apex of the heart, a kind of whorl or vortex, of spiral muscular fibres easily distinguishable when the organ is in active motion. Any muscular fibre arranged in this direction

Fig. 106.

BULLOCK'S HEART, anterior view, showing the superficial muscular fibres.

Fig. 107.



CONVERGING SPIRAL FIBRES AT THE APEX OF THE HEART. The direction of the arrows indicates that of the rotating movement of the heart at the time of the ventricular systole.

[1] Works of William Harvey, M.D., Sydenham Edition. London, 1847, p. 32.

necessarily tends, at the moment of its contraction, to straighten or untwist the spiral. At the time of the ventricular contraction, therefore, the apex of the heart rotates upon its axis, from left to right anteriorly and from right to left posteriorly. This twisting movement at the apex is very perceptible at each pulsation of the heart when exposed in the living animal.

The *impulse* of the heart is a stroke, more or less forcible, of the apex of the organ against the walls of the chest, taking place at the time of the ventricular systole. This impulse is readily perceptible externally, as a general rule, both to the eye and to the touch. In the human subject, when in the erect position, it is located in the fifth intercostal space, midway between the left edge of the sternum and a line drawn perpendicularly through the left nipple; while in the supine position of the body, the heart subsides, in a measure, from the anterior part of the chest, so that its external impulse may become for the time very faint, or may even disappear altogether.

This alternate recession and advance of the apex of the heart, corresponding with its relaxation and contraction, is visible in the organ when exposed by opening the walls of the chest. According to the description given by Harvey, at the time of its motion "the heart is erected, and rises upward to a point, so that at this time it strikes against the breast and the pulse is felt externally." If we allow the end of the finger to rest lightly upon the apex of the exposed heart, the protrusion of this part of the organ at the time of the ventricular systole is distinctly felt, lifting the finger at each beat with a somewhat forcible impulse; and if a light rider of white paper be placed upon the apex, it is also seen to be thrown forward and backward at each alternate contraction and relaxation of the heart.

The immediate cause of the protrusion of the heart's apex at the time of the ventricular systole has been variously regarded, first as an actual elongation of the ventricle, and secondly, as a forward movement of the whole heart, due to a recoil from the blood expelled from it under pressure, or to a reaction of the distended arteries at its base. Galen, who was the first to study the action of the heart by inspection in the living animal, found the transverse diameter of the organ increased during relaxation and its length diminished, while during the systole its width was diminished and its length increased.[1] Of subsequent observers, some believed the heart to be lengthened, others that it was shortened at the time of the ventricular systole. Nearly all the more recent physiological writers of eminence (Longet, Carpenter, Flint, Ranke, Burdon-Sanderson) are of the opinion that the ventricles when contracting diminish in size in every direction, that the apex of the organ approaches the base, but that the whole heart is thrown forward by the impulse of recoil above mentioned. Prof. Flint[2] cut out the heart suddenly from

[1] Galen, De Usu Partium, vi. 8.
[2] Physiology of Man. New York, 1866, p. 189.

the dog, and, fastening it upon a table by needles passed through its base, found the ventricles shortened in contraction; and obtained the same result, in another experiment, by pinning the heart, in the chest of the living animal, to a thin board placed underneath. On the other hand, Drs. Pennock and Moore, who performed a series of very careful experiments upon the action of the heart in sheep, calves, and horses,[1] observed an elongation of the organ at the time of the ventricular systole. They operated by stunning the animals with a blow upon the head, opening the chest, and keeping up artificial respiration, and they were able to measure the extent of elongation by means of a shoemaker's rule applied to the heart.

In our own observations on this point, many times repeated, we have always seen reason to believe that the heart actually elongates in the ventricular systole, and that it is not simply thrown forward by an impulse of recoil. The appearances presented, when viewing the front of the mammalian heart, as it lies in its natural position in the chest, are somewhat complicated. The anterior surface of the organ is mainly occupied by the right ventricle and especially by that portion of it known as the conus arteriosus. This is in reality a vaulted channel running obliquely over the front of the heart, from right to left and from below upward, toward the origin of the pulmonary artery. Its muscular fibres, on the other hand, run directly across it and at right angles to the axis of its cavity, namely, from right to left and from above downward, constituting the most superficial fibres of the heart in this situation. At the time of ventricular systole, these fibres contract across the line of the conus arteriosus, become thickened and more prominent and approximate the base of the heart and the lower border of the conus arteriosus toward each other.

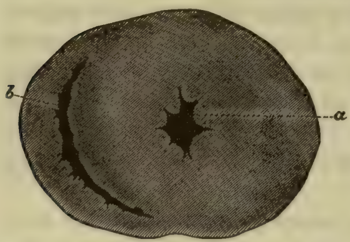
But the right ventricle constitutes a comparatively small portion of the heart. The greater part of its mass is formed by the thick walls of the left ventricle, which occupies a posterior position, and is not fully seen in a front view of the organ. If the heart be tilted up and viewed from its posterior surface, at every contraction its sides will be seen to approximate and its point to elongate; in other words, its transverse diameter diminishes, while its longitudinal diameter increases. Its base may be firmly held by the fingers placed upon the large vessels, while this change of form of the organ is observed. Even in an anterior view, with the whole heart securely held in this position, according to our observations, the apex, at each systole, will rise toward an ivory rod placed horizontally above it, and will recede in the same degree at each diastole.

If this be true, the explanation of the ventricular elongation is readily found in the arrangement of the muscular fibres of the left ventricle. The left ventricle preponderates so much in mass over the other parts of the organ, that its changes of figure determine those of the entire heart.

[1] Philadelphia Medical Examiner, 1839, No. 44.

A transverse section of the heart, in its contracted condition, shows the relative volume of the muscular walls of the right and left ventricles, and the difference in form of the two cavities.

Fig. 108.



TRANSVERSE SECTION OF THE BULLOCK'S HEART IN THE STATE OF CADAVERIC RIGIDITY.—*a.* Cavity of the Left Ventricle. *b.* Cavity of the Right Ventricle.

The left ventricle forms a thick muscular tube, with its cavity nearly in the centre of the cardiac mass; while the right ventricle has the appearance of a comparatively inconsiderable layer of fibres, attached to the lateral surface of the organ, and enclosing a cavity of a more linear and flattened form.

The surperficial cardiac fibres, which make the visible part of the wall of the right ventricle, run obliquely from right to left and from above downward, toward the heart's apex; but the more deeply seated layers, belonging to the left ventricle, take more and more a horizontal or circular course, being wrappped round the ventricle, almost like those of the small intestine. Whenever these muscular fibres contract, they must, of course, swell in the direction of their thickness; and the effect produced by this simultaneous swelling of all the circular fibres is to increase the longitudinal diameter of the ventricle, at the same time that its sides are drawn together and its calibre diminished. In the systole of the ventricle, accordingly, its muscular fibres contract upon its contents, like the fingers of a closed hand, and the blood is expelled from its cavity very much as the fluids of the intestinal canal are forced onward by the contracting circular fibres of the muscular coat.

Fig. 109.

LEFT VENTRICLE OF BULLOCK'S HEART, showing its deep fibres.

Rhythm of the Heart's Action.—The succession of phenomena in the heart's action is peculiar and somewhat complicated. Each pulsation is made up of a double series of contractions and relaxations. The two auricles contract together, and afterward the two ventricles; and in each case the contraction is immediately followed by a relaxation. The auricular contraction is short and feeble, and occupies the first part of the time of a pulsation. The ventricular contraction is longer and more powerful, and occupies the latter part of the same period. Following the ventricular contraction there comes a short interval of repose, after which the auricular contraction again recurs. The auricular and ventricular contractions, however, do not alternate distinctly with each other, like the strokes of the two pistons in a double forcing-pump. On the contrary, they are connected and continuous. The contraction,

which commences at the auricle, is immediately propagated to the ventricle, and runs rapidly from the base of the heart to its apex, very much in the manner of a peristaltic motion, excepting that it is more sudden and vigorous. This part of the heart's action is described by Harvey in very graphic terms, evidently drawn from direct study of the phenomena in the living animal.

"First of all," he says, "the auricle contracts, and in the course of its contraction throws the blood (which it contains in ample quantity as the head of the veins, the storehouse and cistern of the blood) into the ventricle, which being filled, the heart raises itself straightway, makes all its fibres tense, contracts the ventricles, and performs a beat, by which beat it immediately sends the blood, supplied to it by the auricle, into the arteries; the right ventricle sending its charge into the lungs by the vessel which is called vena arteriosa, but which, in structure and function, and all things else, is an artery; the left ventricle sending its charge into the aorta, and through this by the arteries to the body at large.

"These two motions, one of the ventricles, another of the auricles, take place consecutively, but in such a manner that there is a kind of harmony or rhythm preserved between them, the two concurring in such wise that but one motion is apparent, especially in the warmer blooded animals, in which the movements in question are rapid. Nor is this for any other reason than it is in a piece of machinery, in which, though one wheel gives motion to another, yet all the wheels seem to move simultaneously; or in that mechanical contrivance which is adapted to fire-arms, where, the trigger being touched, down comes the flint, strikes against the steel, elicits a spark, which falling among the powder, it is ignited, upon which the flame extends, enters the barrel, causes the explosion, propels the ball, and the mark is attained; all of which incidents, by reason of the celerity with which they happen, seem to take place in the twinkling of an eye."

The above description indicates precisely the manner in which the contraction of the ventricle follows successively and yet continuously upon that of the auricle. The contraction begins, as already stated, at the auricle. Thence it runs immediately forward to the apex of the heart. The entire ventricle contracts vigorously, its walls harden, its apex protrudes, strikes against the walls of the chest, and twists from left to right, the auriculo-ventricular valves shut back, the first sound is produced, and the blood is driven into the aorta and pulmonary artery. These phenomena occupy about one-half the time of pulsation. Then the ventricle is relaxed, and a short period of repose ensues. During this period the blood flows from the large veins into the auricle, and through the auriculo-ventricular orifice into the ventricle; filling the ventricle, by a kind of passive dilatation, about two-thirds or three-quarters full. Then the auricle contracts with a quick motion, forces the last drop of blood into the ventricle, distending it to its full capa-

city; and lastly the ventricular contraction takes place, driving the blood into the large arteries. These movements continue to alternate with each other, and form, by their recurrence, the successive cardiac pulsations.

The Arterial Circulation.

The arteries are a series of branching tubes, which commence with the aorta and ramify throughout the body, distributing the blood to the various vascular organs. They consist of three principal coats, namely, an *inner* coat, composed of thin elastic laminæ lined with a single layer of narrow, elongated and flattened epithelium cells; a *middle* coat, composed of elastic tissue and unstriped muscular fibres, running transversely, or in a circular direction, round the calibre of the vessel; and an *external* coat, consisting mainly of a more or less condensed layer of connective tissue. The principal anatomical distinction between the larger and the smaller arteries is in the structure of their middle coat. In the smaller arteries this coat is composed exclusively of muscular fibres, arranged in one or several layers. In arteries of medium size the middle coat contains both muscular and elastic tissue; while in those of the largest calibre it consists of elastic tissue alone. The large arteries, accordingly, possess a remarkable degree of elasticity and but little contractility; while the smaller are contractile, and less distinctly elastic.

Movement of the Blood through the Arterial System.—The movement of the blood through the arteries is due to the muscular force of the heart and the impulse derived from the ventricular systole. The arterial system, which is an extensive ramification of tubular canals, may be regarded as a great vascular cavity, subdivided from within outward by the successive branching of its vessels, but communicating freely with the heart and aorta at one extremity, and with the capillary plexus at the other, and filled everywhere with the circulating fluid. At the time of the heart's contraction, the muscular walls of the ventricle close in upon its cavity; and as the auriculo-ventricular valves at the same time shut back and prevent regurgitation, the blood is forced out from the ventricle through the aortic orifice. As the ventricle relaxes it is again filled with blood from the auricle, and delivers it, as before, by a new contraction, into the arteries. It is by these impulses, recurring at short intervals, that the entire blood moves in a direction from the heart outward through the arterial system.

Distension of the Arteries by the Heart's Action; Arterial Pulse.—At each ventricular systole a charge of blood is driven into the arteries, distending their walls by the pressure of the additional quantity of fluid introduced into their cavities. When the ventricle afterward relaxes, this active distending force is suspended; and the elastic arterial walls, reacting upon their contents, would drive the blood back into the heart were it not for the closure of the semilunar valves, which shut together

and prevent any movement in a backward direction. The blood is thus urged onward, under the pressure of the arterial elasticity, into the capillary system. When the arteries have become partially emptied, and have returned to their previous dimensions, they are again distended by another contraction of the heart. In this manner a succession of expansions is produced, which can be felt throughout the body wherever the arterial ramifications penetrate. This phenomenon is known by the name of the arterial *pulse*.

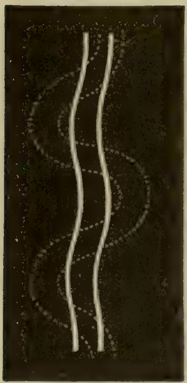
Since each arterial expansion is produced by a ventricular systole, the pulse, as felt in any superficial artery, is a convenient guide for ascertaining the frequency and regularity of the heart's action. The radial artery at the wrist, owing to its easily accessible situation, is mainly employed for this purpose. Any increase or diminution in the frequency of the heart's action is accompanied by a similar change in the arterial pulsations; and alterations in the force or regularity of the cardiac movements are also indicated by corresponding modifications of the pulse at the wrist.

The average frequency of the pulse in the human subject is, for the adult male in a state of quiescence, 70 beats per minute. This rate may be more or less accelerated by any muscular exertion. Even the difference of muscular effort between the positions of standing, sitting, and lying down, will make a normal difference in the pulse of from 8 to 10 beats per minute. Age has a very marked influence on the rapidity of the pulse; it being found, as a rule, more rapid the younger the subject of observation. According to Dr. Carpenter, the pulse of the fœtus, before birth, is about 140, and that of the newly-born infant 130. During the first, second, and third years it gradually falls to 100; by the fourteenth year to 80; and is only reduced to the adult standard by the twenty-first year. At every age, mental excitement may produce a temporary acceleration of the pulse, varying in degree with the peculiarities of the individual.

As a general rule, the rapidity of the heart's action is in inverse ratio to its force; that is, a slow pulse, within physiological limits, is a strong one; a rapid pulse is a feeble one. This is readily noticeable in experiments upon the lower animals, where the force of the heart's action may be measured by the arterial impulse; and where an increase in the frequency of the cardiac pulsations is almost invariably accompanied by a diminution in their strength. The same thing is true in cases of increased frequency of the heart's action from morbid causes; the pulse in febrile or chronic affections becoming weaker as it grows more rapid. An excessive rapidity of the pulse is an indication of great danger; and, in the adult male, a continuous pulse of 160 per minute is almost invariably a fatal symptom.

Increased Curvature of the Arteries in Pulsation.—When the blood is driven by the ventricular systole into the arteries, these vessels are not only distended laterally, but are elongated as well as widened,

Fig. 110.



Elongation and increased curvature of an ARTERY IN PULSATION.

becoming enlarged in every direction. Especially in arteries having a distinctly curved or serpentine course, this elongation and increase of curvature may be observed at the time of each pulsation. It is perceptible, for instance, in emaciated persons, in the temporal artery, or even in the radial at the wrist, and may readily be seen in the mesenteric arteries in the abdomen of the living animal. At every contraction of the heart, the curves of the vessel on each side become more strongly pronounced. In the case of the radial or other artery, running over a bony surface, the vessel may even partially rise out of its bed at each pulsation. In old persons the arterial curvatures become permanently enlarged from frequent distension; and all the arteries tend to assume, with the advance of age, a more serpentine and spiral course.

Time of the Arterial Pulse.—The shock of an arterial pulsation, as perceived by the finger, varies a little in time, according to its distance from the centre of the circulation. If we place one finger upon the chest over the apex of the heart, and another over the carotid artery at the middle of the neck, we can distinguish little or no difference in time between the two impulses; the distension of the carotid being sensibly simultaneous with the heart's contraction. But if the second finger be placed upon the temporal artery, instead of the carotid, there is a perceptible interval between the two beats. The impulse of the temporal artery is felt to be a little later than that of the heart. The pulse of the radial artery at the wrist also appears to be a little later than that of the carotid, and that of the posterior tibial at the ankle joint a little later than that of the radial. The greater the distance from the heart at which the artery is examined, the later is the pulsation perceived by the finger laid upon the vessel.

But it has been conclusively shown that this difference in time of the arterial pulsations, in different parts of the body, is rather relative than absolute. The impulse is communicated at the same instant to all parts of the arterial system; but the apparent difference between them, in this respect, depends upon the fact, that, although all the arteries *begin* to be distended at the same moment, yet those nearest the heart are expanded suddenly, while for those at a distance the distension takes place more gradually. The impulse given to the finger marks the condition of *maximum distension* of the vessel; and this condition occurs at a later period, according to the distance of the artery from the heart.

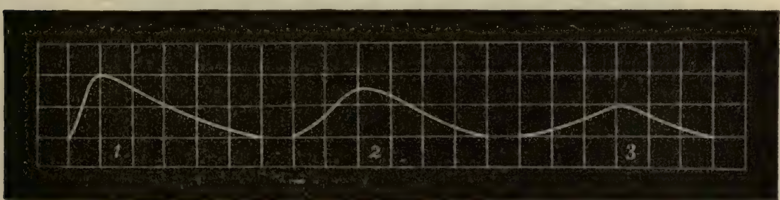
The contraction of the left ventricle is a brisk and sudden motion. The blood driven into the arterial system, meeting with a certain amount of resistance from that already filling the vessels, does not instantly displace a quantity equal to its own mass, but a certain proportion of its force is used in expanding the distensible walls of the vessels. In

the immediate neighborhood, therefore, the expansion of the arteries is sudden and momentary, like the contraction of the heart itself. But this expansion requires for its completion a certain expenditure, both of force and time; so that at a little distance farther on, the vessel is distended neither to the same degree nor with the same rapidity. At the more distant point the arterial impulse is less powerful and arrives more slowly at its maximum.

On the other hand, when the heart becomes relaxed, the artery in its immediate neighborhood reacts upon the blood by its own elasticity; and as it meets with no other resistance than that of the blood in the smaller vessels beyond, it drives a portion of its own blood into them, and thus supplies to these vessels a certain degree of distending force even in the intervals of the heart's action. Thus the difference in size of the carotid artery, at the two periods of the heart's contraction and relaxation, is very marked; for the degree of its distension is great when the heart contracts, and its own reaction afterward empties it of blood to a considerable extent. But in the small branches of the radial or the ulnar artery, there is less distension at the time of the cardiac impulse, because this force has been partly expended in overcoming the elasticity of the larger vessels; and there is less emptying of the vessel afterward, because it is still kept partially filled by the reaction of the aorta and its larger branches.

These facts have been illustrated by Marey,[1] by attaching to the pipe of a small forcing pump, worked by alternate strokes of the piston, a long elastic tube open at its farther extremity. At different points upon this tube are placed small movable levers, which are raised by the distension of the tube whenever water is driven into it by the forcing pump. Each lever carries upon its extremity a small pencil, which marks upon a strip of paper, moving with uniform rapidity, the lines produced by its alternate elevation and depression. By these curves both the extent and rapidity of distension of different parts of the elastic tube are accurately registered. The curves thus produced are as follows:

Fig. 111.



Curves of Pulsation in an Elastic Tube.—1. Near the distending force. 2. At a distance from it. 3. Still farther removed.

From these experiments it is shown that the distension produced by the stroke of the forcing pump begins at the same moment throughout

[1] Journal de la Physiologie. Paris, Avril, 1859

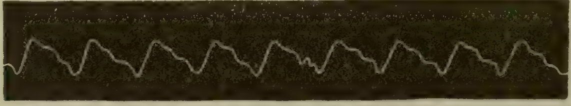
the entire length of the tube, and that the whole time of a pulsation is everywhere of equal duration. But near the commencement of the tube, the expansion is wide and sudden, and occupies only a sixth part of the entire pulsation, while all the rest is taken up by a slow reaction. At more remote points the period of expansion becomes longer and that of collapse shorter; until finally, at a certain distance, the amount of expansion is reduced one-half, and at the same time the two periods are completely equalized.

Automatic Registration of the Arterial Pulse; the Sphygmograph.— The frequency and characters of the arterial pulse may be permanently recorded by the use of a movable lever capable of registering its own oscillations, and so arranged that it may be applied to any of the superficial arteries in the living body. This instrument, which was first made practically serviceable by the improvements of Marey, is the *sphygmograph.* It consists of a small ivory plate, which is gently pressed upon the artery by means of a fine spring, and which thus rises and falls with each expansion and collapse of the arterial tube. The motion of the plate is communicated to a vertical metallic rod touching the under surface of the registering lever near its attached extremity. The oscillating extremity of the lever, when the instrument is in operation, thus follows the movements of the ivory plate, and registers faithfully upon the strip of paper, the frequency and form of the arterial pulsations.

The advantage of this instrument is, first, that the length of the lever magnifies to the eye the extent of the arterial oscillations, and thus enables us to perceive movements too delicate to be distinguished by the touch alone; and, secondly, that, each part of a pulsation being permanently registered upon paper, the most evanescent changes in the form of the artery may be afterward studied at leisure and compared with each other.

By the use of the sphygmograph it is shown, that, while there is a general resemblance in the form of pulsation of different arteries, nearly every vessel to which the instrument can be applied presents certain peculiarities dependent on its size, position, and distance from the heart. In the radial artery at the wrist, each pulsation consists of a

Fig. 112.



TRACE OF THE RADIAL PULSE, taken by the Sphygmograph.

sudden expansion of the vessel, indicated by a rapid upward movement of the lever, making, in the trace, a straight, nearly vertical line. This is followed by a gradual descent corresponding with the collapse of the artery, until it reaches the lowest point of the trace, when the movement of ascension again takes place, and so on alternately. The line of descent, however, is not straight, like that of ascension, but is marked

by one, and sometimes by two or even three slight undulations, indicating a corresponding variation in the tension of the artery during its period of collapse.

The undulations in the line of descent, in the sphygmograph tracing, are due to an oscillation in the mass of the blood, subsequent to the impulse of the heart, and during the reaction of the arterial system. Marey has shown, by a series of well-conducted experiments,[1] that similar oscillations are produced when any incompressible liquid is driven by a sudden impulse into an elastic tube; and that they are indicated by a similar movement of the index of the sphygmograph. When the heart's impulse is moderate, and the tension of the arterial system fully developed, the undulations in the descending line of the pulse are only slightly perceptible; but when the heart's impulse is more rapid, and the arterial tension diminished, the undulations become more marked. Marey found that he could procure upon his own person traces of different form, in this respect, by simply increasing the temperature of the body by the addition of warmer clothing. The following are three traces of the radial pulse obtained in this way, by increasing the quantity of clothing at intervals of twenty minutes.

Fig. 113.

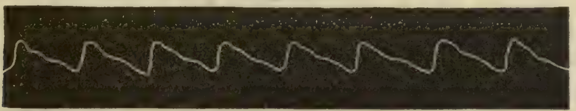


Fig. 114.

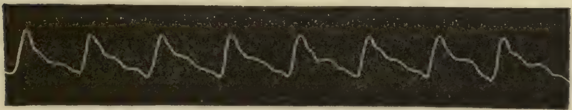
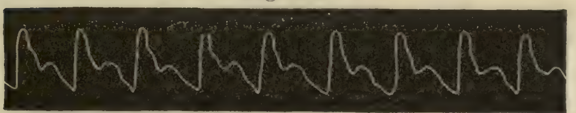


Fig. 115.



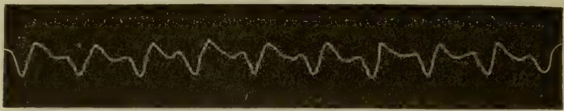
Variations of the Radial Pulse, under the influence of increased temperature. (Marey.)

Dicrotic Pulse.—In certain conditions, accompanied by rapid pulsation of the heart with greatly diminished arterial tension, the rebound or oscillation of the artery becomes so marked, in proportion to the original impulse, that it is easily perceived by the finger, and thus the pulse is apparently reduplicated; that is, there are two pulsations of the artery for each contraction of the heart, namely, one due to the original impulse, and another due to the oscillation of the blood in the

[1] Physiologie Médicale de la Circulation du Sang. Paris, 1863, p. 266.

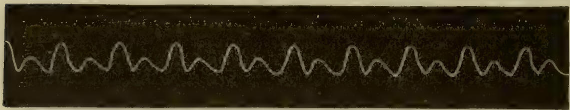
feebly distended artery. This is the *dicrotic* pulse, which is often present in diseases of a typhoid character.

Fig. 116.



Dicrotic Pulse of Typhoid Pneumonia. (Marey.)

Fig. 117.



Dicrotic Pulse of Typhoid Fever (Marey.)

It is evident that the dicrotic character of the pulse is not, in reality, peculiar to diseased conditions, since the sphygmograph shows that it exists more or less perfectly in a state of health; only it is too slight in degree to be appreciated by the finger.

Koschlakoff[1] has succeeded in verifying the results obtained from the sphygmograph, and in demonstrating the mechanism of the dicrotic pulse. He shows that if a liquid be driven by a rapid impulse through an elastic tube, connected with two separate pressure gauges, one situated near the point of entrance of the liquid, the other near its point of exit, the liquid will rise in the first gauge before the increased pressure reaches the second; that it then falls while the second is rising, and again rises while the second falls; showing an alternate increase and diminution of pressure in the two extremities of the elastic tube. This alternation continues until the pressure is equalized, or until the tube is again distended by a new impulse.

Pulsating Movement of the Blood in the Arterial System.—Owing to the alternate contraction and relaxation of the heart, the blood passes through the arteries in a series of impulses; and the hemorrhage from a wounded artery is distinguished from venous or capillary hemorrhage by the fact that the blood flows in successive jets, as well as more rapidly and abundantly. If a slender canula be introduced through the walls of the left ventricle, in the exposed heart of a living animal, the flow of blood from its external orifice is seen to be completely intermittent. A strong jet takes place at each ventricular contraction, and at each relaxation the flow is interrupted. If a puncture be made, however, in any of the large arteries near the heart, the flow of blood through the opening is no longer intermittent, but continuous; only it is much stronger at the time of the ventricular contraction, and diminishes, though it does not entirely cease, at the time of relaxation. If the blood were driven through rigid and unyielding tubes, its flow would

[1] In Lorain Etudes de Médecine Clinique. Paris, 1870, p 75

be everywhere intermittent; and it would be delivered from an orifice situated at any point, in perfectly interrupted jets. But the arteries are yielding and elastic; and this elasticity moderates the force of the separate arterial pulsations, and partially fuses them with each other. The effect of this is to produce, in the larger and medium-sized arteries, a movement of the blood which is increased in rapidity and volume at each cardiac impulse, and diminished in the interval of relaxation.

Equalization of the Blood-current in the peripheral parts of the Arterial System.—It has already been shown that the distensible and elastic properties of the arterial walls have the effect of making the flow of blood more continuous than it would be if subjected only to the intermitting action of the heart. A part of the force of each cardiac pulsation is absorbed for the time in the distension of the artery; and this force is again returned in the form of an impulse to the blood at the following interval, by the elastic reaction of the vessel. The farther from the heart the blood recedes, the greater becomes the influence of the intervening arteries; and thus the remittent or pulsating character of the arterial current, which is strongly pronounced in the vicinity of the heart, becomes gradually diminished during its passage through the vessels, until in the smaller arteries, like the labials, it is hardly perceptible to the unaided eye.

The physical influence of an elastic medium, in equalizing the force of an interrupted current, may be shown by forcing water from a syringe alternately through two tubes, one of India rubber, the other of glass or metal. Whatever be the length of the inelastic tube, the water thrown into one extremity will be delivered from the other in distinct jets, corresponding with the strokes of the piston: but if the metallic tube be replaced by one of India rubber of sufficient length, the elasticity of this substance merges the separate impulses into each other, and the water is discharged from the farther extremity in a continuous stream.

The elasticity of the arteries never entirely equalizes the force of the separate pulsations, since a pulsating character can be seen in the flow of the blood through even the smallest arteries, if examined under the microscope; but this pulsating character diminishes from the heart outward, and the current becomes much more continuous in the smaller vessels than in the larger arteries or in those of medium size.

The Arterial Pressure.—The arterial circulation, as shown by the above facts, is not an entirely simple phenomenon, but is the combined result of two different physical forces. It is due, first, to the intermitting action of the heart, by which the blood is driven in successive impulses from within outward; and, secondly, to the elasticity of the entire arterial system, by which it is subjected to a continuous pressure.

If any one of the larger or medium sized arteries be divided, in the living animal, and a glass tube of the same diameter securely fixed in its open orifice and held in the vertical position, the blood will at once rise in the tube to a height of five and a half or six feet, and will con-

tinue to oscillate at or about this level. The height of the column of fluid, thus supported outside the body, indicates the degree of pressure to which the blood is subjected in the interior of the vessels. This pressure, due to the reaction of the entire arterial system, is known as the *arterial pressure.*

The arterial pressure is best measured by connecting the open artery, by a flexible tube, with a small reservoir of mercury, provided with a narrow upright glass tube, open at its upper extremity. When the mercury in the receiver is exposed to the pressure of the arterial blood, it rises in the upright tube to a corresponding height.

This pressure averages, in the dog and other animals of similar size, 150 millimetres of mercury.

When such an instrument is connected with the carotid artery, the level of the mercury in the upright tube, while indicating on the whole an average pressure, exhibits two series of oscillations; showing that the degree of the blood-pressure is constantly changing, owing to two different causes. One of these oscillations is synchronous with the *movements of respiration.* At every inspiration, the level of the mercury falls somewhat, with every expiration it rises. As the movement of inspiration consists in an expansion of the cavity of the chest, its effect is to diminish the support afforded the heart and great bloodvessels, and of course to lower in a similar degree the tension of the whole arterial system. At the moment of expiration, on the other hand, the thoracic parietes return to their former position, and the pressure upon the heart and the arteries in the chest is re-established. These changes are indicated by corresponding slow fluctuations in the arterial pressure and in the height of the mercurial column. The oscillations of the mercury due to respiration, however, are not at all uniform, but vary according to the condition of the respiratory movements. When respiration is active and somewhat labored, the oscillations may reach the extent of 30 millimetres; when it is very quiet, as in an animal deeply etherized, they may diminish so far as to be nearly or quite imperceptible.

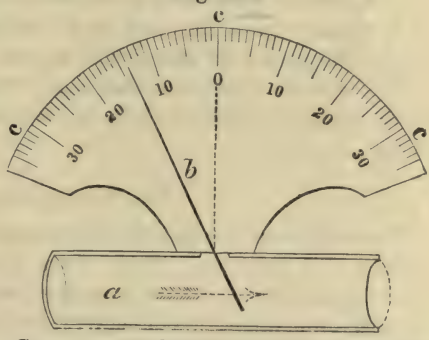
The other series of oscillations is a more constant one and is due to the *cardiac pulsations.* It consists of comparatively rapid undulations of the mercurial column, simultaneous with the movements of the heart. At every contraction of the ventricle, the mercury rises from 12 to 15 millimetres, and at every relaxation it falls to its previous level. Thus the instrument becomes a measure, not only for the constant pressure of the arteries, but also for the intermitting pressure of the heart; and on that account it has received the name of the *cardiometer.* It is seen, accordingly, that each contraction of the heart is superior in force to the resistance of the arteries by nearly one-tenth; and the arterial system is, therefore, kept filled by successive cardiac pulsations, and the arterial tension maintained, notwithstanding that the blood is constantly being discharged from the arteries into the capillary circulation.

Velocity of the Arterial Current.—The rapidity with which the blood moves in the arterial tubes is much greater than in any other part of the

vascular system. Its exact rate varies somewhat according to the situation of the vessel and the period of the pulsation. Its velocity is greatest in the immediate neighborhood of the heart, and diminishes as the blood recedes from the centre of the circulation. The successive division of the aorta and its primary branches into smaller and smaller ramifications increases the extent of surface of the arterial walls with which the blood comes in contact. The adhesion produced by this contact, as well as the mechanical obstacle arising from the frequent division of the vessels and the separation of the streams, contributes to retard the current, which accordingly becomes perceptibly slower in the small arteries than in those of larger or medium size. In the smallest arteries, as examined by the microscope in the transparent tissues, the partial adhesion of the blood to the vascular wall, and the greater rapidity of its flow in the axis of the vessel are readily perceptible. The consistency of the circulating fluid, however, and the smoothness of the internal surface of the arteries, are such that this obstacle to the movement of the blood has only a very partial influence in retarding its flow; and even in the smallest arteries it is so rapid, when seen under the microscope, that the shape of the separate blood-globules cannot be distinguished, but only a mingled current shooting forward with increased velocity at each cardiac pulsation.

The average rapidity of the blood stream in the larger arteries, in dogs, horses, and calves, was determined by Volkmann, as 30 centimetres per second. The most exact experiments on this point are those of Chauveau.[1] He experimented by introducing into the carotid artery of the horse a brass tube with thin walls, about five centimetres long and eight or nine millimetres in diameter. The tube was introduced through a longitudinal incision in the walls of the exposed vessel, and secured in position by a ligature near each extremity; so that the arterial current would pass, without serious obstruction, through the brass tube forming, for the time, a part of the arterial walls. In the side of the tube was a small opening, three millimetres long by one and a half millimetre wide, closed by an elastic membrane properly secured so as to prevent the escape of the blood. Through the centre of the elastic membrane there was passed a very light metallic

Fig. 118.



CHAUVEAU'S INSTRUMENT, for measuring the rapidity of the arterial current.—*a*. Brass tube, introduced into the calibre of the artery. *b*. Index-needle passing through the elastic membrane in the side of the brass tube, and moving by the impulse of the blood-current. *c*. Graduated scale, for measuring the extent of the oscillations of the needle.

[1] Journal de la Physiologie, Paris, Octobre, 1860, p. 695.

needle, the inner extremity of which, somewhat flattened in shape, projected into the interior of the vessel, and received the impulse of the arterial blood; while the outer portion, prolonged into a slender index, marked upon a semicircular graduated scale the oscillations of the inner extremity, and consequently the varying rapidity of the arterial current. The actual velocity, indicated by any given oscillation of the needle, was ascertained beforehand by attaching the apparatus to an elastic tube and passing through it a stream of warm water of known rapidity.

Chauveau found, by these experiments, that the details of the circulatory movement differ somewhat in the larger arteries near the heart from those in the smaller branches farther removed.

a. In the carotid artery, at the instant of the systole of the heart, the blood is suddenly put in motion with a high degree of rapidity, amounting on the average to a little over fifty centimetres per second.

At the termination of the systole, and immediately before the closure of the aortic valves, the movement of the blood decreases considerably, and may even, for the time, be completely arrested.

At the instant of closure of the aortic valves, the circulation receives a new impulse, and the blood again moves forward with a velocity of rather more than 20 centimetres per second.

Subsequently, the rapidity of the current diminishes gradually during the period of the heart's inaction, until, at the end of this period and just before a new systole, it is reduced, on the average, to 15 centimetres per second.

b. In the smaller arterial branches, such as the facial, the movement of the arterial current is more uniform. It is less rapid at the moment of the heart's systole; and on the other hand, it is always more active during the period of ventricular repose.

The secondary impulse, following the closure of the aortic valves, is much less perceptible than in the larger arteries, and may even be altogether absent.

The Venous Circulation.

The veins are composed, like the arteries, of three coats; an inner, middle, and exterior. They differ from the arteries in containing a much smaller quantity of muscular and elastic fibres, and a larger proportion of condensed connective tissue. They are consequently more flaccid and compressible than the arteries, and less elastic and contractile. They are furthermore distinguished, throughout the limbs, neck, and external portions of the head and trunk, by being provided with valves, arranged in the form of festoons, and so placed as to allow the blood to pass readily from the periphery toward the heart, while they prevent its reflux in the opposite direction.

Although the walls of the veins are thinner and less elastic than those of the arteries, yet their capacity for *resistance to pressure* is equal, or even superior, to that of the arteries. Milne Edwards has collected the

results of various experiments, which show that the veins will sometimes resist a pressure which is sufficient to rupture the walls of the arteries.[1] In one instance the jugular vein supported, without breaking, a pressure equal to a column of water 148 feet in height; and in another, the iliac vein of a sheep resisted a pressure of more than four atmospheres. The portal vein was found capable of resisting a pressure of six atmospheres; and in one case, in which the aorta of a sheep was ruptured by a pressure of 72 kilogrammes, the vena cava of the same animal supported a pressure equal to 80 kilogrammes.

This property of the veins is to be attributed to the abundance of white fibrous tissue in their composition; the same tissue which forms nearly the whole of the tendons and fasciæ, and which is distinguished by its density and unyielding nature.

The *elasticity* of the veins, on the other hand, is much less than that of the arteries. When filled with blood, they enlarge to a certain size; and when cut across and emptied, their sides simply collapse and remain in contact with each other.

Another peculiarity of the venous system consists in its numerous *independent and communicating channels.*

In injected preparations, two, three, or more veins are often to be seen coming, together, from the same region of the body, and presenting frequent transverse communications. The deep veins accompanying the brachial artery inosculate freely with each other, and also with the superficial veins of the arm. In the veins coming from the head, the external jugulars communicate with the thyroid veins, the anterior jugular, and the brachial veins. The external and internal jugulars commuicate with each other, and the two thyroid veins also form an abundant plexus in front of the trachea.

Thus the blood, coming from the extremities toward the heart, flows, not in a single channel, but in several; and as these channels communicate freely with each other, the blood passes most abundantly sometimes through one of them, and sometimes through another.

Movement of the Blood through the Venous System.—The flow of blood through the veins is less powerful and regular than that through the arteries. It depends on the combined action of three different physical forces.

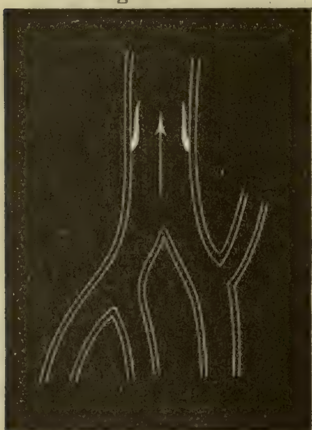
I. The most constant and important of these forces is the *pressure of the blood from the capillary circulation.* The blood moves from the arteries into and through the capillary vessels, under an impulse derived originally from the contractions of the heart, and converted by the elasticity of the arterial walls into a more or less steady and uniform pressure. This pressure is not entirely exhausted in carrying the blood through the narrow channels of the capillary system; and it accordingly emerges from these vessels and enters the commencement of the veins with a certain amount of force sufficient to fill the venous rootlets

[1] Leçons sur la Physiologie. Paris, 1859, tome iv. p. 301.

and to pass thence into the larger branches and trunks of the venous system. As the veins converge from the periphery toward the centre, and unite into branches of larger calibre, the resistance afforded by contact of the circulating fluid with their inner surfaces constantly diminishes from without inward; and every contraction of the right ventricle, accompanied by the closure of the tricuspid valve, expels a certain quantity of venous blood, and thus relieves the returning current from the obstacle of its accumulation. As the pressure of the blood from the capillaries continues uniform, and as the resistance to it is incessantly neutralized by the action of the right ventricle, it forms the most simple and effective cause for the movement of the blood through the venous channels.

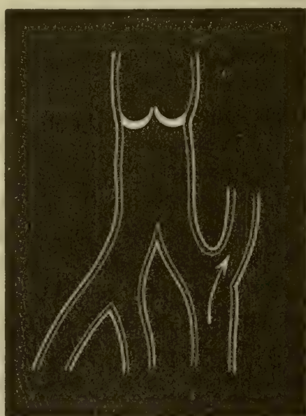
II. The flow of the blood through the veins is also aided in great measure by the *contraction of the voluntary muscles.* The veins which convey the blood through the limbs, and the parietes of the head and trunk, lie among voluntary muscles which are more or less constantly in a state of alternate contraction and relaxation. At every contraction these muscles become swollen laterally, and thus compress the veins situated between them. The blood, expelled from the vein by this pressure, cannot regurgitate toward the capillaries, owing to the venous valves, which shut back and prevent its reflux. It is accordingly forced onward toward the heart; and when the muscle relaxes and the vein is liberated from pressure, it is again filled from behind, and the circulation goes on as before.

Fig. 119.



VEIN with valves open.

Fig. 120.



VEIN with valves closed; stream of blood passing off by a lateral channel.

This force is very efficient in maintaining the venous circulation; since the voluntary muscles are more or less active in every position of the body, and the veins are thus alternately subjected to compression and relaxation. The entire voluntary muscular system acts in this way by communicating to the venous current indirect impulses of frequent

repetition, which, combined with the action of the valves, urge the blood from the periphery toward the heart.

III. A third cause, which is more or less active in promoting the movement of the venous blood, is the *force of aspiration* exerted by the thorax. When the chest expands by the lifting of the ribs and the descent of the diaphragm, this movement tends to diminish the pressure upon its contents, and consequently to draw into the thoracic cavity any fluids which can gain access to it. The expanded cavity is principally filled by the atmospheric air, which passes in through the trachea to fill the bronchial tubes and the pulmonary vesicles. But the blood in the neighboring parts of the venous system is solicited at the same time, though to a less degree, in a similar direction. This force of aspiration, like the respiratory movements themselves, is gentle and uniform in character. Its influence extends indirectly throughout the venous system, each expansion of the chest causing an increased flow of blood from the extra- to the intra-thoracic veins, while the former are filled up from behind as fast as they are emptied in front.

Rapidity of the Venous Circulation.—With regard to the velocity of the venous current, no direct results have been obtained by experiment. Owing to the flaccidity of the veins, and the readiness with which the flow of blood through them is disturbed, it is not possible to determine this point, in the same manner as it has been determined for the arteries. The only calculation which has been made in this respect is based upon a comparison of the total capacity of the arterial and venous systems. As the same blood which passes outward through the arteries returns inward through the veins, the rapidity of its flow in each direction must be in inverse proportion to the capacity of the two systems. The capacity of the entire venous system, when distended by injection, is about twice as great as that of the entire arterial system. During life, however, the venous system is at no time so completely filled with blood as is the case with the arteries; and, making allowance for this difference, it may be estimated that the entire quantity of venous blood is to the entire quantity of arterial blood nearly as three to two. The velocity of the venous blood, as compared with that of the arterial, is therefore as two to three; and if we regard the average rapidity of the arterial current, according to Volkmann's experiments, as 30 centimetres per second, this would give the movement of blood in the large veins as about 20 centimetres per second. This calculation, however, is altogether an approximative one; since the venous circulation varies, according to many different circumstances, in different parts of the body. It may nevertheless be considered as expressing with sufficient accuracy the general relative velocity of the arterial and venous currents in corresponding parts of their course.

The Capillary Circulation.

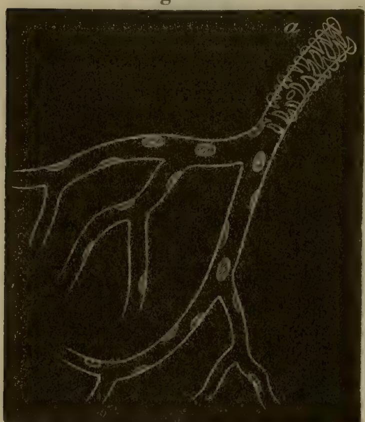
The capillary bloodvessels are minute inosculating tubes, which permeate the vascular organs in various directions, and bring the blood into

indirect contact with the substance of the tissues. They are continuous with the terminal ramifications of the arteries on the one hand, and with the commencing rootlets of the veins on the other. They vary somewhat in size in the different organs and tissues, their average diameter in the human subject being about 10 mmm., or $\frac{1}{100}$ of a millimetre. The largest capillaries, according to Kölliker, in the glands and the osseous tissue, may reach the diameter of 15 mmm.; while the smallest, in the muscles, the nerves, and the retina, are 4.5 mmm., that is, almost exactly the size of the smallest of the red globules of the blood.

As the arterial ramifications approach the confines of the capillary system they diminish gradually in size, and lose first their external coat of connective tissue. Their middle coat at the same time becomes reduced to a single layer of fusiform muscular fibres, which become in turn less numerous, and lastly disappear altogether. The vascular canal is thus finally composed only of a single tunic continuous with the internal coat of the arterial ramifications.

The capillary bloodvessel, examined in its recent condition, as extracted from any soft vascular tissue, appears to consist of a simple, nearly homogeneous tubular membrane, provided with flattened oval nuclei placed at more or less regular distances from each other, and projecting slightly into the cavity of the vessel.

Fig. 121.



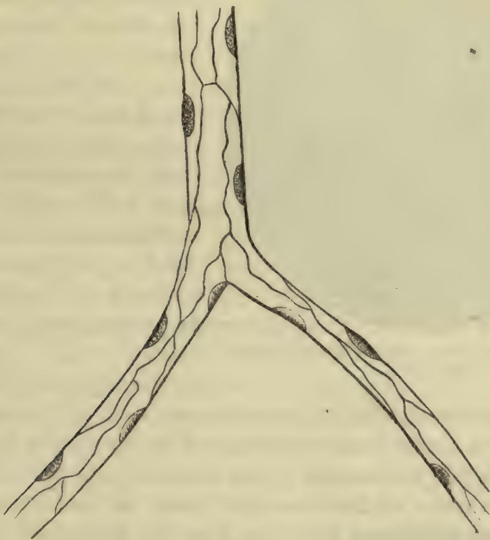
Small Artery, with its muscular tunic (*a*) breaking up into capillaries. From the *pia mater*.

It has been found, however, that if a capillary bloodvessel be treated with a weak solution of silver nitrate, its inner surface becomes marked off into regular spaces, each of which includes a nucleus; indicating that its apparently homogeneous tunic is composed of flattened epithelium-like cells, united with each other at their adjacent edges by an intervening cement. It is this thin layer of intervening substance which becomes darkened by the action of the silver nitrate and thus brings into view the outlines of the cells forming the vascular wall.

The form of the cells constituting the vascular membrane varies in different regions and in capillaries of different calibre. According to Kölliker, in the smallest capillary bloodvessels, measuring from 4.5 to 7 mmm. in diameter, the cells are narrow, elongated, and fusiform, as in Fig. 122; often curled from side to side, so as to form each a half cylinder, two of them joining at their edges to complete the capillary tube, and alternating longitudinally, the pointed extremity of one cell being intercalated between those of the two following cells. In

the larger capillaries, of 8 to 13 mmm. in diameter, where the calibre of the vessel is surrounded by three or four cells placed side by side, they are shorter and wider in form, like those of ordinary pavement epithelium. The arrangement of these microscopic forms in the wall of the

Fig. 122.



CAPILLARY BLOODVESSEL, from the tail of the tadpole; showing the outlines of its epithelium-like cells, rendered visible by the action of silver nitrate. (Kölliker.)

capillary bloodvessels has given rise to the opinion, entertained by some histologists, that the vascular system is to be regarded as a series of intercellular canals, provided, in different regions, with varying additional layers of muscular, elastic, and connective tissue.

The capillary bloodvessels are further distinguished from both arteries and veins by their frequent inosculation. The arteries constantly divide and subdivide, as they pass from within outward, while the veins as constantly unite with each other, to form larger and less numerous branches and trunks, as they converge from the periphery toward the centre; and although the arteries always present inosculations in certain regions, and the veins more frequently still, this feature is, nevertheless, a secondary or incidental one in both vascular systems. The arteries are essentially diverging tubes to distribute the blood from within outward; the veins are converging channels to collect and transport it from without inward.

The capillaries, on the other hand, are mainly characterized by their constant and repeated intercommunication. They are vascular canals which penetrate the solid organs and tissues, uniting with each other at

short intervals, in such a manner as to form an interlacing network or plexus of minute bloodvessels, known as the *capillary plexus.* The vessels forming this plexus vary somewhat in size, abundance, and arrangement in different parts of the body. In every vascular organ and tissue there are certain spaces or islets, inclosed on all sides by capillaries, but into the interior of which these vessels do not penetrate. Such islets or intervascular spaces must therefore obtain their nourishment by the exudation and absorption of the fluid ingredients of the blood through the capillary walls and the substance of the intervening tissue.

Fig. 123.

CAPILLARY PLEXUS, from the web of the frog's foot.

The special arrangement of the capillary bloodvessels, and the form and size of the meshes of their network, are, in general, characteristic of each separate organ or tissue. In the muscles, the meshes are in the form of long parallelograms, corresponding with that of the muscular fibres; in the mucous membranes of the stomach and large intestine, they are hexagonal, or irregularly circular, inclosing the orifices of the secreting follicles; in the papillæ of the tongue and skin, and in the placental tufts, the capillaries form twisted vascular loops; in the glomeruli of the kidneys, convoluted coils; in the connective tissue, irregularly shaped figures, corresponding in direction with the fibrous bundles of the tissue.

The capillary bloodvessels are the most abundant, and interlaced in the finest network, in those organs to which the blood is distributed for other purposes than for local nutrition; as for that of aeration, secretion, or absorption. One of the closest of all the capillary networks is that of the lungs, in which the diameter of the spaces separating the bloodvessels, in the walls of the pulmonary vesicles, is sometimes a little greater and sometimes a little less than that of the capillaries themselves. In the glandular tissue of the liver, the spaces separating the adjacent vessels are only a little wider than the capillaries forming the intra-lobular network. In the nerves, the serous membranes, and the tendons, on the other hand, the capillary vessels are less closely interwoven; and in the adipose tissue they form wide, open meshes, embracing the exterior of the separate fat vesicles.

Movement of the Blood in the Capillary Vessels.—The motion of the blood in the capillaries may be studied by examining, under the microscope, any transparent tissue of a sufficient degree of vascularity. The frog is the most convenient animal for this purpose, owing to the readi-

ness with which the circulation may be maintained even in the internal organs, exposed at ordinary temperatures. In order to secure immobility, the medulla oblongata may first be broken up by a strong needle introduced through the cranium, or the voluntary muscles may be paralyzed by the subcutaneous injection of six drops of a filtered watery solution of woorara, made in the proportion of one part to five hundred. The whole body, with the exception of the part used for observation, should be enveloped in a light linen or cotton bandage, kept moistened to prevent desiccation of the surface. The tongue, or the web of one foot, may be stretched over a glass side, and placed under the lens of the instrument. To examine the pulmonary circulation, an opening should be made in one side just behind the anterior limb, and the lung moderately inflated through the glottis, until it protrudes through the external wound. For the mesenteric circulation, an incision should be made in the left flank of a male frog, a loop of intestine carefully drawn out of the abdomen, and the mesentery allowed to rest upon a circular glass plate, 12 millimetres in diameter, and 6 millimetres in thickness, cemented upon a large glass plate, by which the body of the animal is supported. Under favorable circumstances the circulation will go on in either of these organs for several hours.

When the circulation is examined in this manner, the smaller arteries, the capillary vessels, and the minute veins are often visible under the microscope in the same region. The blood can be seen entering the field by the smaller arteries, shooting through them with great rapidity in successive impulses, and flowing off by the veins at a somewhat slower rate. In the capillaries, the circulation is considerably less rapid than in either the arteries or the veins. It is also perfectly steady and uninterrupted in its flow. The blood moves through its vascular channels in a uniform current, without their exhibiting any appearance of contraction or dilatation. Another marked peculiarity of the capillary circulation is that it has no definite direction. Its numerous streams pass indifferently above and below each other, at right angles to each other's course, or even in opposite directions; so that the blood, while in the capillaries, circulates everywhere among the tissues, in such a manner as to be distributed to all parts of their substance.

Fig. 124.

Capillary Circulation in web of frog's foot.

The motion of the red and white globules is also peculiar, and shows

distinctly the difference in their physical properties. In the larger vessels the red globules are carried along in close column, in the central part of the stream; while near the edges of the vessel there is a transparent space occupied only by clear plasma, in which no red globules are to be seen. In the smaller vessels the globules pass two by two, or follow each other in single file. The flexibility and semi-fluid consistency of the red globules are very apparent from the readiness with which they become folded up, bent or twisted, and with which they glide through minute branches of communication, smaller in diameter than themselves. The white globules, on the other hand, move more slowly through the vessels. They drag along the external portions of the current, and are sometimes temporarily arrested, adhering for a few seconds to the internal surface of the vessel. Whenever the current is obstructed or retarded, the white globules accumulate in the affected portion, and become more numerous there in proportion to the red.

It is during the capillary circulation that the blood serves for the nutrition of the vascular organs. Its fluid portions transude through the walls of the vessels, and are absorbed by the tissues in the proportions requisite for their nourishment, or for the products of secretion; while its albuminous ingredients are also transformed into new materials, characteristic of the different tissues and fluids. In this way are produced the myosine of the muscles, the collagen of the bones, tendons, and ligaments, the ptyaline of the saliva, and the pepsine of the gastric juice; and in the lungs, the exchange of oxygen and carbonic acid takes place in the capillary vessels. The blood in the capillary circulation thus furnishes, directly or indirectly, the materials of nutrition for the entire body.

Physical Cause of the Capillary Circulation.—The physical conditions which influence the movement of the blood in the capillaries are somewhat different from those of the arterial and venous circulations. By the successive division of the arteries from the heart outward, the movement of pulsation is to a great extent equalized in the smaller arterial branches. But as these vessels reach the confines of the capillary system, they suddenly break up into a terminal ramification of still smaller and more numerous vessels, and so lose themselves at last in the capillary network. By this final increase of the vascular surface, the equalization of the heart's action is completed. There is no longer any pulsating character in the force which acts upon the circulating fluid; and the blood moves through the capillary vessels under a continuous and uniform pressure.

This pressure is sufficient to cause the blood to pass with considerable rapidity through the capillary plexus, into the commencement of the veins. This fact was first demonstrated by Sharpey,[1] who employed an injecting syringe with a double nozzle, one extremity of which was con-

[1] Todd and Bowman, Physiological Anatomy and Physiology of Man, vol. ii. p. 350.

nected with a mercurial gauge, while the other was inserted into the artery of a recently killed animal. When the syringe, filled with defibrinated blood, was fixed in this position, the defibrinated blood would press with equal force upon the mercury in the gauge and upon the fluid in the bloodvessels; and thus the height of the mercurial column indicated the amount of pressure required to force the defibrinated blood through the capillaries of the animal, and to make it return by the corresponding vein. In this way Prof. Sharpey found that, when the free end of the injecting tube was attached to the mesenteric artery of the dog, a pressure of 90 millimetres of mercury caused the blood to pass through the capillaries of the intestine and of the liver; and that under a pressure of 130 millimetres, it flowed in a full stream from the divided extremity of the vena cava.

We have obtained similar results by experimenting upon the vessels of the lower extremity. A full grown healthy dog was killed, and one of the lower extremities immediately injected with defibrinated blood, by the femoral artery, in order to prevent coagulation in the smaller vessels. A syringe with a double flexible nozzle was then filled with defibrinated blood, and one extremity of its injecting tube attached to the femoral artery, the other to the mouthpiece of a cardiometer. By making the injection, it was then found that the defibrinated blood was returned from the femoral vein in a continuous stream under a pressure of 120 millimetres, and that it was discharged very freely under a pressure of 130 millimetres.

Since the arterial pressure upon the blood during life is equal to 150 millimetres of mercury, it is evident that this pressure is sufficient to propel the blood through the capillary circulation.

Furthermore, the blood is not altogether relieved from the influence of elasticity, after leaving the arteries. For the capillaries themselves have a certain degree of elasticity, and are surrounded, in addition, by the tissues of the organs in which they are distributed; many of which, such as the lungs, spleen, skin, lobulated glands, and mucous membranes, contain elastic fibres more or less abundantly disseminated through their substance. The effect of this physical property, in the vessels and the neighboring parts, may be exhibited in artificial injections of one of the lower limbs through the femoral artery, or of the liver through the portal vein. If, while the parts are distended by the fluid passing through their vessels, the injecting force be suddenly arrested, the movement of the current does not at once cease, but the fluid of injection continues to escape for several seconds from the femoral or hepatic vein, owing to the continuous pressure exerted from behind. The elasticity of the surrounding tissues, therefore, supplements that of the minute bloodvessels, and aids in producing a uniform movement of the capillary circulation.

Velocity of the Blood in the Capillary Vessels.—The motion of the blood in the capillary vessels is much less rapid than in either the arteries or the veins. It may be measured, with a tolerable approach

to accuracy, during the microscopic examination of transparent and vascular tissues. The results obtained in this way by different observers (Valentin, Weber, and Volkmann), show that the rate of movement of the blood through the capillaries is rather less than one millimetre per second; or about 5 centimetres per minute. Since the rapidity of the current must be in inverse ratio to the entire calibre of the vessels through which it moves, it appears that the united calibre of all the capillaries must be not less than 300 times greater than that of the arteries. It does not follow from this, however, that the whole quantity of blood contained in the capillaries at any one time is so much greater than that in the arteries; since, although the united *calibre* of the capillaries is large, their *length* is very small. The effect of the anatomical structure of the capillary system is to disseminate a comparatively small quantity of blood over a very large space, so that the physiological reactions necessary to nutrition take place with promptitude and energy. Although the rate of movement of the blood in these vessels, accordingly, is a slow one, yet as the distance to be passed over between the arteries and veins is very small, the blood requires but a short time to traverse the capillary system, and to commence its returning passage by the veins.

General Rapidity of the Circulation.

The rapidity with which the blood passes through the *entire round of the circulation* has been demonstrated by Hering, Poisseuille, Matteucci, and Vierordt in the following manner: A solution of potassium ferrocyanide was injected into the right jugular vein of a horse, at the same time that a ligature was placed upon the corresponding vein on the left side, and an opening made in it above the ligature. The blood flowing from the left jugular vein was then received in separate vessels, which were changed every five seconds, and the contents afterward examined. It was thus found that the blood drawn from the first to the twentieth second contained no traces of the ferrocyanide; but that which escaped from the vein at the end of from twenty to twenty-five seconds, showed unmistakable evidence of the presence of the foreign salt. The potassium ferrocyanide must, therefore, during this time, have passed from the point of injection to the right side of the heart, thence to the lungs and through the pulmonary circulation, to the left side of the heart by the pulmonary veins, outward by the arteries to the capillary circulation of the head and neck, and must have again commenced its downward passage to the heart by the opposite jugular vein.

By extending these observations, it was found that the duration of the circulatory movement varies to some extent in different species of animals; being, as a general rule longer in those of larger size. The main result, as given by Milne Edwards,[1] is as follows:

[1] Leçons sur la Physiologie. Paris, 1859, tome iv. p. 364.

DURATION OF THE CIRCULATORY MOVEMENT.

In the Horse	28 seconds.
" Dog	15 "
" Goat	13 "
" Rabbit	7 "

These results are corroborated by subsequent investigations. In experimenting upon the dog, by injecting a solution of potassium ferrocyanide into the jugular vein, and immediately drawing blood from the corresponding vein on the opposite side, we have found that the short interval of time requisite for closing the first vein by ligature after terminating the injection, and opening the second in such a manner as to obtain a specimen of blood for examination, is sufficient to allow of the passage of the ferrocyanide through the entire round of the circulation. If we regard the duration of this movement in the human subject as intermediate between that in the dog and the horse, making allowance for the difference in size, this would give the time required by the blood to make the circuit of the veins, arteries, and capillaries, in man, as not far from 20 seconds.

Local Variations in the Capillary Circulation.

An important class of phenomena connected with this part of the subject consists of the *local variations* in the capillary circulation. These variations are often very marked, and show themselves in many different parts of the body. The pallor or suffusion of the face under mental emotion, the congestion of the mucous membranes during digestion, and the local and defined redness of the skin produced by any irritating application, are all instances of this sort. These changes are due to the contraction or dilatation of the smaller arterial branches which supply the part with blood, under the influence of nervous action. The middle coat of these vessels is composed mainly of organic or unstriped muscular fibres, arranged in a transversely circular direction, which by their contraction diminish and by their relaxation enlarge the calibre of the arterial tube. They regulate, accordingly, by this means, the quantity of blood passing to the capillary system. When contracted, they resist more strongly the impulsive force of the arterial current, and admit the blood in smaller quantity. When dilated, they allow a freer access to the capillaries and the blood passes in greater abundance.

These changes are most distinctly manifested in the periodical congestion of the glandular organs. All the glands and mucous membranes connected with the digestive apparatus enter into a state of unusual vascular excitement at the time of secretion and digestion. This can readily be seen, in the living animal, in the pancreas, and in the mucous membranes of the stomach and small intestine; the tissues of these parts being visibly redder and more turgid during digestion and absorption than in the fasting condition.

A similar variation of the circulation has been particularly studied

by Bernard[1] in the submaxillary gland of the dog. During the ordinary condition of glandular repose he found that it required sixty-five seconds to obtain five cubic centimetres of blood from the submaxillary vein; but, when the gland was excited to functional activity, the same quantity of blood was discharged by the vein in fifteen seconds. Thus the volume of blood passing through the organ in a given time was more than four times as great while the gland was in a state of active secretion, as in a condition of repose.

The increased flow of blood, in a secreting gland, is accompanied also by an important change in its appearance. During repose, the blood, which enters the submaxillary gland from the arteries bright red, is changed in its tissue from arterial to venous, and passes out by the veins of a dark color. But when the secretion of the gland is excited, either by galvanization of its nerve or by introducing vinegar into the mouth of the animal, the blood is not only discharged in larger quantity, but passes out red by the veins, so as hardly to be distinguished in color from arterial blood. When the secretion of the gland is suspended, the blood in its vein again becomes dark-colored as before. There is little doubt that the same is true of most of the secreting glands, and that the blood circulating in their capillaries is changed from red to blue only during the period of functional repose; while at the time of active secretion it not only passes through the vessels in greater abundance, but also retains its ruddy color in the veins.

This is because, during the period of glandular repose, the blood performs in its tissues the usual functions of nutrition. It therefore undergoes the ordinary changes and becomes altered in color from arterial to venous. But the period of active secretion is a period of congestion, during which the blood passes in larger quantity, while its watery and saline ingredients exude into the secretory ducts, bringing with them the materials accumulated in the interval of repose. There is nothing in this process to exhaust the oxygen of the blood or to change its color from arterial to venous, and it therefore passes into the veins comparatively unaltered.

A similar ruddy color of venous blood is to be seen in the renal veins, where it is often nearly identical with that of arterial blood. The difference in hue between the renal veins and the neighboring muscular veins or the vena cava, when exposed by opening the abdomen of the living animal, is very marked, provided the kidneys be at the time in a state of functional activity. The greater part of the blood traversing these organs is changed only by the elimination of its urea and the remaining ingredients of the urine, which exude into the excretory tubules. The process of active local nutrition is here altogether subservient to the discharge of organic materials already existing in the blood; and the loss of oxygen and alteration in color of the circulating fluid are thus comparatively insignificant.

[1] Leçons sur les Liquides de l'Organisme. Paris, 1859, tome ii. p. 272.

On the other hand, the venous blood coming from the muscular tissue is very dark colored, especially if the muscles be in a state of active contraction. As the muscles form so large a part of the entire mass of the body, their condition has a preponderating influence upon the color of the venous blood in general. The greater the activity of the muscular system, the darker is the color of the blood returning from the trunk and extremities. When the muscles are in a state of repose or paralysis, on the contrary, the change is less marked; and in the complete relaxation produced by abundant hemorrhage or by complete etherization, the blood in the veins often approximates in color to that in the arteries.

Fig. 125.

Diagram of the Circulation.—1. Heart. 2. Lungs. 3. Head and upper extremities. 4. Spleen. 5. Intestine. 6. Kidney. 7. Lower extremities. 8. Liver.

Finally, in the lungs the reverse process takes place. In these organs the blood is supplied with a fresh quantity of oxygen, to replace that which has been consumed elsewhere; and accordingly it changes its color from dark purple to bright red as it passes through the pulmonary capillaries.

Both the physical and chemical phenomena, therefore, of the circulation vary at different times and in different organs. The actions which go on throughout the body, are varied in character, and produce a similar difference in the phenomena of the circulation. The venous blood, consequently, has a different composition as it returns from different organs. In the parotid gland it yields the ingredients of the saliva; in the kidneys those of the urine. In the intestine it absorbs the nutritious elements of the digested food; and in the liver it gives up substances destined to produce the bile, while it absorbs glucose from the hepatic tissue. In the lungs it changes from blue to red, and in the capillaries of the general system, from red to blue; and its temperature, also, varies in different veins, according to the peculiar chemical and nutritive changes going on in the organs from which they originate.

CHAPTER XVI.

THE LYMPHATIC SYSTEM.

In addition to the connected series of canals by which the blood passes in a continuous round through the arteries, capillaries, and veins, there is also a system of vessels, leading only from the periphery toward the centre, and discharging into the great veins near the heart the fluids which have been absorbed in the solid tissues of the body. The fluid contained in these vessels is nearly or quite colorless, especially in thin layers, and from its transparent and watery appearance is called the "lymph," and the vessels themselves constitute what is known as the *lymphatic system.*

As the blood circulates through the capillaries under the influence of the arterial pressure, certain of its ingredients transude through the vascular walls and penetrate the interstices of the anatomical elements of the tissues. An increased pressure upon the blood, either from arterial congestion or from obstruction to the venous current, will increase the amount of transudation, producing an œdematous condition of the part, which is first perceptible in the loose connective tissue, but which may afterward involve the more compact substance of the organs. In the normal state of the circulation, this interstitial fluid, which is the real source of nutrition for the solid parts, does not, however, stagnate in contact with them, but is renewed by a continual change. As fresh supplies need to be drawn from the circulating blood, the older portions are removed by absorption and returned to the centre of the circulation by the lymphatic vessels. Thus these vessels may be considered as complementary in their function to the veins. The blood, containing the red globules, requires to be rapidly and abundantly returned to the lungs by the veins, in order to regain the oxygen necessary for its continued vitality; while the lymphatics collect more gradually the fluids which have served for the slower process of nutrition and growth.

Anatomical Structure and Arrangement of the Lymphatic System.

In structure the lymphatics do not essentially differ from the bloodvessels, their principal peculiarity being that their walls are more delicate and transparent. This circumstance, together with the colorless nature of their contents, renders them less easily recognizable by dissection. Those of larger and medium size consist of three coats, similar, in general characters, to the corresponding tunics of the bloodvessels. According to the observations of Kölliker, the external coat alone is distinguished from that of the veins by the possession of smooth mus-

cular fibres which are arranged in a longitudinal and oblique direction; a character which is to be seen in lymphatics of 0.2 millimetre in diameter and upward. Like the veins, they are provided with numerous valves, opening toward the heart and closing toward the periphery, the vessel often presenting a well-marked dilatation just within the situation of the valves. The smallest lymphatics consist of only a single coat, composed of flattened, epithelium-like, nucleated cells, which may be brought into view, like those of the capillary bloodvessels, by the staining action of a silver nitrate solution.

Origin and Course of the Lymphatic Vessels.—So far as the origin of the lymphatics has been demonstrated by injections, these vessels commence in the substance of the tissues by plexuses. They are more abundant in organs which are fully supplied with bloodvessels, and are absent in tissues where bloodvessels do not exist, such as those of the cornea, the vitreous body, and the epithelial coverings of the skin and mucous membranes. According to Von Recklinghausen, the meshes of the lymphatic plexus, as a general rule, are intercalated between those of the capillary bloodvessels; so that the point of junction of two or more lymphatics is always in the middle of the space surrounded by the adjacent bloodvessels. Thus the lymphatic capillary is situated at the greatest distance possible from the nearest capillary bloodvessels; and in the transudation of fluids from one to the other, the intervening substance of the tissue will always be completely traversed by the nutritious ingredients of the blood. In membranous expansions presenting a free surface, as in the skin and mucous membranes, the plexus of capillary bloodvessels is invariably nearer the surface, while the lymphatics occupy a deeper plane beneath it. Even in the villi of the small intestine, the network of bloodvessels is situated immediately under the epithelial layer, and surrounds the lacteal vessel which is placed in the central part of the villus.

Beside the lymphatic capillaries proper, certain irregularly shaped spaces or canals, containing only a colorless or serous fluid, have been found in organs consisting of condensed connective tissue, like the central tendon of the diaphragm and muscular fasciæ. They have been demonstrated mainly by the process of treating the tissues with a solution of silver nitrate, which stains the solid portions of a dark color, but leaves the capillary vessels and the serous canals uncolored. These interstitial spaces or serous canaliculi have been regarded by some observers (Recklinghausen) as directly continuous with the lymphatic capillaries, and as constituting the immediate sources of supply for the lymph; but this connection is not universally admitted. The serous canaliculi are distinguished from the lymphatic capillaries by their much smaller size, and by the fact that they do not possess, like the latter, a lining of epithelial cells.

From their plexuses of origin the lymphatic vessels pass inward toward the great channels and cavities of the body, uniting into larger branches and trunks, and following generally the course of the prin-

cipal bloodvessels and nerves. Those of the lower extremities enter the cavity of the abdomen, and join with the lymphatics of the abdominal organs to form the commencement of the thoracic duct, which ascends through the cavity of the chest, receiving branches from the thoracic organs to the root of the neck, where it is joined by lymphatics from the left side of the head and the left upper extremity, and terminates in the left subclavian vein, at the point of its junction with the left internal jugular. The lymphatics coming from the right side of the head and neck, the right upper extremity, and a portion of the thoracic organs, form a trunk of smaller size, the right lymphatic duct, which terminates in the right subclavian vein at its junction with the right internal jugular. Thus the lymph, collected from the vascular tissues of the entire body, is mingled with the venous blood a short distance before its arrival at the right side of the heart.

The Great Serous Cavities of the Body are Lymphatic Lacunæ.—It is well known that in the amphibious reptiles there are irregularly-shaped spaces or lacunæ, forming a part of the lymphatic system and interposed between adjacent organs in various parts of the body. In the mammalia the peritoneal and pleural cavities, and probably all the principal serous sacs, are also in direct communication with the lymphatic vessels. This was first shown by Recklinghausen[1] for the peritoneal cavity of the rabbit, which communicates by microscopic orifices with the lymphatic vessels in the central tendon of the diaphragm. These communications were demonstrated in two ways: First, on injecting into the peritoneal cavity of the animal milk, or a watery fluid holding in suspension minute granules of coloring matter, the lymphatic vessels of the central tendon of the diaphragm were afterward found to be filled with the white or colored injection. Secondly, the central tendon of the diaphragm being carefully removed from the recently killed animal, and a drop of milk placed upon its peritoneal surface, the milk globules could be directly observed under the microscope, running in converging currents to certain points on the surface of the tendon and there penetrating into its lymphatic vessels. The cavity of the pleura has also been found by similar means to communicate with the lymphatic vessels in its neighborhood. The serous cavities accordingly are either extensive lacunæ, forming in some regions the origin of the lymphatic vessels, or else they are wide but shallow expansions of the cavity of the lymphatics, situated at various points in their course.

The Lymphatic Glands.—During the passage of the lymphatic vessels from the periphery toward the centre, they are repeatedly interrupted by ovoid, glandular-like bodies, of a pale reddish color and somewhat firm consistency, varying in size from about two to twenty millimetres in their long diameter. They do not exist in fish and reptiles, but are always present in birds and mammalia. As a rule, several lymphatic vessels reach these bodies, coming in a direction from the periphery; and

[1] Stricker's Manual of Histology, Buck's Edition. New York, 1872, p. 221.

several others leave them at another portion of their surface, passing onward toward the centre of the circulation. The former are called the "afferent," the latter the "efferent" lymphatic vessels. Owing to the general glandular-like aspect which they present to the eye, these bodies are known as lymphatic "glands," although they possess no proper excretory duct, and whatever new materials are formed in their interior must be carried away either by the veins or by the efferent lymphatic vessels.

The lymphatic glands are situated upon the course of the lymphatic vessels on the inside of the limbs at the flexures of the joints, in the axilla and the groin, in the thoracic and abdominal cavities, along the sides of the spinal column, in the mesentery, and in the sides and anterior part of the neck.

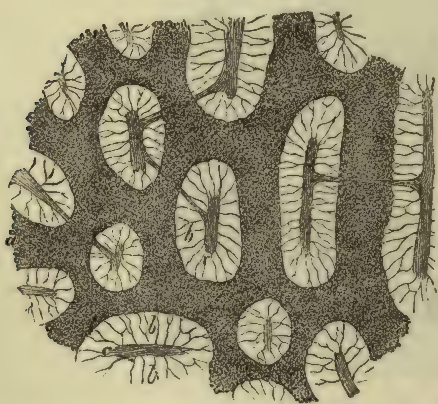
Fig. 126.

LYMPHATIC VESSELS AND GLANDS OF THE HEAD, NECK, AND THORAX.—1. Thoracic duct, at the point of its emergence from the chest. 2. The same duct, at its junction with the left subclavian vein. (Mascagni.)

As regards the structure of the lymphatic glands they consist, First, of an external fibrous envelope, which sends from its internal surface prolongations in the form of septa and branching bands into the deeper parts of the gland, so that the interior of the organ is divided into a

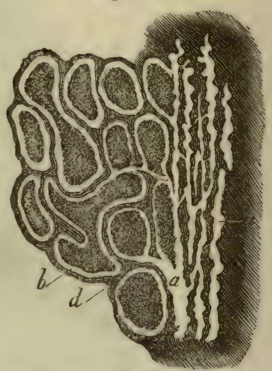
multitude of smaller spaces by the inosculations of this fibrous framework. The bands constituting this framework are called the "trabeculæ." Secondly, in the interstices between the trabeculæ there is situated the pulpy substance of the gland. In the more external or cortical part of the gland, the interspaces have a rounded or sac-like form, which gives to this portion of the organ a granular aspect, while this appearance is wanting in the deeper or medullary portion; but in both situations the glandular pulp has essentially the same microscopic texture. Thirdly, the bloodvessels of the gland penetrate it from the outside, usually at a depressed spot called the "hilum," and, after reaching the interior, break up into a rich plexus of capillaries. These bloodvessels and their capillary plexus follow distinct routes in the gland, in the middle of the spaces between the trabeculæ. The capillary bloodvessels are surrounded and held in position by very fine branching fibres attached to their external surface; and in the meshes of these fibres, as well as between the bloodvessels, there are imbedded a great number of rounded, granular, nucleated cells, about 9 mmm. in diameter, similar to the white globules of the blood and of the lymph, and which in this situation are known as "lymph globules." The presence of these granular cells, fixed between and immediately around the capillary bloodvessels, gives to the parts occupied by them a well-marked opaque appearance by transmitted light; and there are thus formed, in a thin section of the gland, elongated, opaque tracts or cords, separated by intervening transparent spaces, and communicating with each other at frequent intervals.

Fig. 127.



Thin Section of a Lymphatic Gland from the Ox.—*a.* Medullary cords. *b.* Lymph paths. *c.* Trabeculæ. (Kölliker.)

Fig. 128.



Longitudinal Section through the hilum of a mesenteric gland from the ox, showing the commencement of the efferent lymphatic vessels injected from a puncture of the glandular substance.—*a.* Plexus of efferent vessels. *b.* Lymph paths. *c.* Medullary cords. *d.* Trabeculæ. (Kölliker.)

These opaque and vascular tracts are called the *medullary cords* of the lymphatic gland. They are the only vascular parts of the organ; as the capillary bloodvessels never pass beyond them into the intervening transparent spaces. The transparent spaces, situated between the

medullary cords and immediately surrounding the trabeculæ, constitute the *lymph-paths*, or the channels by which the lymph traverses the glandular substance from the afferent to the efferent vessels. The afferent lymphatic vessels, according to the united testimony of more recent observers, after ramifying upon the outer surface of the gland, penetrate its fibrous envelope and become continuous with the transparent portions of the glandular substance. This has been shown by injections of the lymphatic gland from the afferent vessels; and Kölliker has also demonstrated a similar connection of the same channels with the efferent vessels, by injecting these vessels from the substance of the gland.

The lymph-paths present a transparent appearance in thin sections of the gland for the reason that the granular lymph-cells which they contain are easily detached and removed by manipulation, while those of the medullary cords are more firmly fixed in the fibrous mesh-work and do not readily yield to a displacing force. It has been found by Kölliker that a watery or serous fluid, injected through the substance of the gland under very moderate pressure, will also displace these cells and leave the spaces which they occupied nearly clear. For these reasons it is regarded as certain that the lighter spaces in the lymphatic glands are, as their name indicates, the channels by which the lymph passes from the afferent to the efferent vessels, and that the lymph-cells are detached by this current from the place of their growth and carried onward through the rest of the lymphatic system.

Transudation and Absorption by the Animal Tissues.

During the passage of the blood through the capillary bloodvessels a variety of actions take place by which some of its ingredients are given up to the tissues by transudation and are at the same time replaced by others derived by absorption from the adjacent parts. The lymphatic system of vessels, furthermore, is entirely filled by the absorption of materials taken up from the surrounding tissues; and the composition of the fluid which they contain depends upon the property, belonging to animal membranes, of transmitting or absorbing certain fluid substances in a peculiar way. This property is exhibited experimentally in the following manner.

If a fresh animal membrane be firmly attached over the mouth of a cylindrical glass tube, filled with pure water and immersed in solutions of various substances, in such a manner that the membrane forms a continuous diaphragm, having the water on one side and the solution on the other, it is found that different substances penetrate the membrane and pass through it to the water with very different degrees of rapidity. As a general rule crystallizable substances, such as mineral salts, glucose, urea, pass with facility; while the non-crystallizable organic matters, such as albumen, starch, gum, pass with comparative difficulty There are certain exceptions, however, to this rule. Thus albumen, under ordinary circumstances, transudes slowly or not at all through animal membranes; while albuminose, which is also non-

crystallizable, passes very rapidly and abundantly. The distinction, furthermore, between the two classes of substances is not a complete one, since they may nearly all be made to transude in some degree by increasing the pressure of the column of fluid upon the corresponding side of the membrane; but the difference between them is often very great in this respect. According to the observations of Liebig,[1] the requisite pressure for different liquids, in passing through the same membrane in a given time, is as follows:

Comparative Pressure Required to Cause Transudation through Ox-bladder.

Kind of liquid.	Height of the mercurial column.
Water	324 millimetres.
Solution of salt	514 "
Oil	920 "
Alcohol	1298 "

Owing to their varying degree of transmissibity through membranes this property has even been employed for the purpose of separating different substances from each other, when mingled together in the liquid form. This process is termed *Dialysis.* Thus, if a solution containing both gum and sugar be placed in contact with one side of the membranous diaphragm, with pure water on the other, the sugar alone will pass through, while the gum will be left behind. If a mixture of albumen and sodium chloride be placed under the same conditions, the salt will transude in a pure form leaving the albumen by itself; both substances in this way being purified from each other through the action of the membrane. By the same process it has been found possible to extricate poisonous crystallizable matters, such as strychnine or arsenious acid, from their admixture with albuminous substances in a state of sufficient purity to allow of their detection by chemical tests. The tissues of an animal membrane, accordingly, may in this way exercise a kind of elective affinity for various substances, and produce a special composition in fluids which have transuded through them.

Endosmosis and Exosmosis.—Beside the elimination of chemical ingredients above described, the phenomena of transudation often give rise to a change in volume of the fluid on either side of the membranous septum. When an animal membrane is interposed between two different liquids which are imbibed and transmitted by it with different degrees of facility, that which passes most readily will accumulate in larger quantity on the opposite side of the membrane.

If we take, for example, a solution of salt and an equal volume of distilled water, and inclose them in a glass tube with a fresh animal membrane stretched between, the two liquids being in contact with opposite sides of the membrane, after a time they will have become

[1] Cited in Longet, Traité de Physiologie. Paris, 1861, tome i. p. 384.

mingled, to a certain extent, with each other. A part of the salt will have passed into the distilled water, giving it a saline taste; and a part of the water will have passed into the saline solution, making it more dilute than before. If the quantities of the two liquids, which have become so transferred, be measured, it will be found that a comparatively large quantity of water has passed into the saline solution, and a comparatively small quantity of the saline solution has passed out into the water. That is, the water passes inward to the salt more rapidly than the salt passes outward to the water. The consequence is, that the saline solution is increased in volume, while the water is diminished. The more abundant passage of the water, through the membrane to the salt, is called *endosmosis;* and the more scanty passage of the salt outward to the water is called *exosmosis.*

The mode usually adopted for measuring the rapidity of endosmosis is to take a glass vessel, shaped somewhat like an inverted funnel, wide at the bottom and narrow at the top. The bottom of the vessel is closed by a thin animal membrane, stretched tightly over its edge and secured by a ligature. From the top of the vessel there rises a narrow glass tube, open at its upper extremity. When the instrument is thus prepared, it is filled with a saline or saccharine solution and placed in a vessel of distilled water; so that the membrane, stretched across its mouth, shall be in contact with pure water on one side and with the interior solution on the other. The water then passes in through the membrane, by endosmosis, faster than the ingredients of the solution pass out. An accumulation consequently takes place inside the vessel, and the level of the fluid rises in the upright tube. The height to which the fluid thus rises in a given time is a measure of the intensity of the endosmosis, and of its excess over exosmosis. By varying the constitution of the two liquids, and the arrangement of the membrane, the variations in endosmotic action under different conditions may be readily ascertained. Such an instrument is called an *endosmometer.*

Physical Conditions influencing Endosmosis.—The conditions which regulate the intensity and extent of endosmosis have been investigated by Dutrochet, Graham, Vierordt, Matteucci, and Cima. The first of these conditions is the *freshness of the animal membrane.* A membrane that has been dried and moistened again, or one that has begun to putrefy, will not produce its full effect. It is also found that if the membrane be allowed to remain and macerate in the fluids, after the column has risen to a certain height in the upright tube, it begins to descend again when putrefaction commences, and the two liquids finally sink to the same level.

The next condition is the *extent of contact* between the membrane and the two liquids. The greater the extent of contact, the more rapid is endosmosis. An endosmometer with a wide mouth will produce more effect than with a narrow one, though the volume of liquid may be the same in both instances. The action takes place in the substance of the membrane, and is proportional to its extent of surface.

The *nature of the membrane* employed, and even its *position in regard to the two liquids*, also influence the result. Different serous and mucous membranes act with different degrees of force. The effect produced is not the same with the integument of different animals, nor with membranous tissues taken from different parts of the body of the same animal. This depends upon the fact that the power of absorption for a given liquid is different in different tissues. Chevreuil investigated this point by taking definite quantities of certain animal substances, and immersing them in various liquids for twenty-four hours, at the end of which time the substance was removed and weighed. Its increase in weight showed the quantity of liquid which it had absorbed. The following table[1] shows the result of these experiments:

COMPARATIVE POWER OF ABSORPTION IN DIFFERENT TISSUES.

100 Parts of		Water.	Saline Solution.	Oil.
Cartilage,	absorb in 24 hours,	231 parts.	125 parts.	
Tendon,		178 "	114 "	8.6 parts.
Elastic ligament,		148 "	30 "	7.2 "
Cornea,		461 "	370 "	9.1 "
Cartilaginous ligament,		319 "		3.2 "
Dried fibrine,		301 "	151 "	

The influence of the position of the membrane depends upon a similar difference in the absorbing power of its two surfaces. With some fluids, endosmosis is more rapid when the membrane has its mucous surface in contact with the dense solution, and its dissected surface in contact with the water. With other substances, the more favorable position is the reverse. Matteucci found that, in using the mucous membrane of the ox-bladder, with water and a solution of sugar, if the mucous surface of the membrane were in contact with the saccharine solution, the liquid rose in the endosmometer between 80 and 113 millimetres in two hours. But if the same surface were turned toward the water, the rise of the column of fluid was only 63 or 72 millimetres in the same time.

Another important circumstance is the *constitution of the two liquids* and their relation to each other. As a general thing, if the liquids employed be water and a saline solution, endosmosis is more active, the more concentrated is the solution in the endosmometer; that is, a larger quantity of water will pass inward toward a dense solution than toward one which is dilute. But the force of endosmosis varies with different liquids, though they may be of the same density. Dutrochet measured the force with which water passes through the mucous membrane of the ox-bladder, into different solutions of the same density, with the following result:[2]

[1] In Longet, Traité de Physiologie. Paris, 1861, tome i. p. 383.

[2] In Matteucci, On the Physical Phenomena of Living Beings. Pereira's translation. Philadelphia, 1848, p. 48.

COMPARATIVE INTENSITY OF ENDOSMOSIS OF WATER TOWARD DIFFERENT LIQUIDS, AS MEASURED BY THE RISE OF THE COLUMN IN THE ENDOSMOMETER.

Endosmosis of water toward	Divisions of the Endosmometer tube.
Solution of gelatine	3
" gum	5
" sugar	11
" albumen	12

The primary cause of this variation in the phenomena of endosmosis is the different absorptive power possessed by an animal membrane or tissue for different liquids. This is partly shown by the experiments of Chevreuil, in which oily matters were usually absorbed less readily than either water or saline solutions. Nearly all animal membranes also absorb water more rapidly than a solution of salt. If a membrane, partly dried, be placed in a saturated solution of sodium chloride, it will absorb the water in so much larger proportion than the salt that a part of the salt will be left behind and deposited in a crystalline form on the surface of the membrane.

When an animal membrane, accordingly, is placed in contact with two different liquids, it absorbs one of them more abundantly than the other; and if that which is absorbed in the greatest quantity is also readily diffused into the liquid on the opposite side, a rapid endosmosis will take place in that direction, and a slow exosmosis in the other. Consequently, the least absorbable fluid increases in volume by the constant admixture of that which is taken up more rapidly. There are even some cases in which endosmosis takes place without being accompanied by exosmosis. This occurs when water and albumen are employed as the two liquids. For while water readily passes inward through the animal membrane, the albumen does not pass out. If an opening be made in the large end of a fowl's egg, so as to expose the shell-membrane, and the whole be then immersed in a goblet of water, endosmosis will take place freely from the water to the albumen, so as to distend the shell-membrane and make it protrude, like a hernia, from the opening in the shell. But the albumen does not pass outward through the membrane, and the water in the goblet remains pure. After a time the pressure from within, due to the accumulation of fluid, becomes so great as to burst the shell-membrane, after which the two fluids mix uniformly with each other.

But a substance like albumen, which will not pass out by exosmosis toward pure water, may traverse a membrane which is in contact with a solution of salt. This has been shown to be the case with the shell-membrane of the fowl's egg, which, if immersed in a watery solution containing from 3 to 4 per cent. of sodium chloride, will allow the escape of a small proportion of albumen. Furthermore, if a mixed solution of albumen and salt be placed in a dialysing apparatus, the salt alone will at first pass outward leaving the albumen; but after the exterior liquid has become perceptibly saline, the albumen also begins to pass in appreciable quantity.

For the same membrane and different solutions of the same substance, the direction and intensity of transudation depend upon the strength of the solutions. With endosmometers containing solutions of sugar or salt, and immersed in pure water, as shown by Dutrochet, the stronger the solution the more rapid is the endosmosis from without; and if two solutions of salt be employed, with a membranous septum between them, endosmosis takes place from the weaker solution to the stronger, and is proportional to the difference in their densities. Density, however, is not always the condition which determines the direction of the current. For although with saline or saccharine solutions the direction of endosmosis is from the lighter to the denser liquid, with alcohol and water it takes place from the water to the alcohol; that is, from the denser to the lighter liquid. It is evident from these facts that the process of endosmosis does not depend principally upon the attraction of the two liquids for each other, but upon *the attraction of the animal membrane for the two liquids.* The membrane is not a passive filter through which the liquids mingle, but is the active agent which determines their transudation. The membrane has the power of absorbing liquids, and of taking them up into its own substance. This property, belonging to the membrane, depends upon the organic ingredients of which it is composed; and, with different animal substances, the rate of absorption is different. The tissue of cartilage, for example, as shown by the experiments of Chevreuil, will absorb more water, weight for weight, than that of the tendons; and the tissue of the cornea will absorb nearly twice as much as that of cartilage.

The continuance of endosmosis is much favored by *renewal of the two liquids.* Since the accumulation of fluid on one side of the membrane depends on the difference in composition of the liquids employed and the consequent difference in their rate of absorption, when endosmosis has been for some time going on, and the two liquids have approximated each other in composition, the activity of endosmosis will be diminished in proportion. As the salt or sugar passes outward to the water and the water inward to the solution in the endosmometer, the external liquid acquires a saline or saccharine ingredient, and the interior solution becomes more dilute; and when the two liquids have thus arrived at the same or nearly the same composition, endosmosis must cease. But if the exterior liquid be constantly replaced by a current of pure water, and the interior solution maintained at its original strength by the addition of new ingredients, the process of transudation will go on with undiminished activity until the membrane has lost its absorbent power. The effect of a constantly renewed current in aiding endosmosis may be readily shown by filling the cleansed intestine of a rabbit with water from a reservoir and then placing it in a shallow glass vessel containing a dilute solution of hydrochloric acid. If the water be allowed to flow through the intestine under pressure from the reservoir, that which is discharged from its open extremity will in a few seconds show the presence of hydrochloric acid by its

reaction with litmus. The acid in this case passes through the wall of the intestine against the pressure of the current, which is of course directed from within outward.

Endosmosis is also regulated, to a great degree, by *temperature.* As a rule it is more active when the temperature is moderately elevated. Dutrochet found that an endosmometer, containing a solution of gum, absorbed only one volume of water at a temperature of 0°, but absorbed three volumes at about 34°. Variations of temperature will sometimes even change the direction of the endosmosis altogether, particularly with dilute solutions of hydrochloric acid. In the experiments of Dutrochet, when the endosmometer was filled with dilute hydrochloric acid and placed in distilled water at the temperature of 10°, endosmosis took place from the acid to the water, if the density of the acid solution were less than 1.020; but from the water to the acid, if its density were greater than this. On the other hand, at the temperature of 22°, the current was from within outward when the density of the said solution was below 1.003, and from without inward when it was above that point.

Absorption and Transudation in the Tissues of the Living Body.— In the experiments above detailed, performed with membranes and tissues taken from the dead body, by which the phenomena of endosmosis and exosmosis were first studied, the phenomena represent imperfectly those which take place in the living organism. The property, belonging to an animal membrane, of determining the absorption or transudation of various liquids, depends upon its organic constitution and is exercised in the greatest intensity during life. In the living body, all the conditions requisite for the acts of endosmosis and exosmosis are present in a higher degree than is possible in any artificial experiment. The membranes and tissues are all perfectly fresh, and unaltered by either desiccation or putrescence; the extent of absorbing surface is indefinitely multiplied by the repeated ramification of the capillary bloodvessels or the glandular tubes; the internal temperature of the body is maintained at a point most favorable for the activity of endosmosis; and finally the continuous movement of the blood and the lymph, in their respective vessels, supplies the ingredients for a constant renewal of the process and at the same time removes the accumulation of the transuded material.

In the living body, accordingly, the transudation of fluids is accomplished with great rapidity. It has been shown by Gosselin, that if a watery solution of potassium iodide be dropped upon the cornea of a living rabbit, the iodine passes into the cornea, aqueous humor, iris, lens, sclerotic and vitreous body, in the course of eleven minutes; and that it will penetrate through the cornea into the aqueous humor in three minutes, and into the substance of the cornea in a minute and a half. In these experiments it is evident that the iodine actually passes into the deeper portions of the eye by simple endosmosis, and is not

transported by the bloodvessels; since no trace of it is to be found in the tissues of the opposite eye, examined at the same time.

The same observer has shown that the active principle of belladonna penetrates the tissues of the eyeball in a similar manner. He applied a solution of atropine sulphate to both eyes of two rabbits. Half an hour afterward, the pupils were dilated. Three-quarters of an hour later, the aqueous humor was collected by puncturing the cornea with a trocar; and this fluid, dropped upon the eye of a cat, produced dilatation and immobility of the pupil in half an hour. These facts show that the aqueous humor of the affected eye actually contains atropine, which it absorbs from without through the cornea, and which thus acts directly upon the muscular fibres of the iris.

But in all vascular organs, the processes of endosmosis and exosmosis are still further accelerated by two important conditions, namely, first, the movement of the blood circulating in the vessels, and secondly, the minute dissemination and distribution of these vessels through the tissues.

If a solution of the extract of nux vomica be injected into the subcutaneous connective tissue of the hind leg of two rabbits, in one of which the bloodvessels of the limb have been left free, while in the other they have been previously tied, so as to stop the circulation of blood in the part, in the first rabbit the poison will be absorbed and will produce convulsions and death in the course of a few minutes; but in the second animal, owing to the stoppage of the local circulation, absorption will be retarded, and the poison will find its way into the general circulation so slowly, that its specific effects will show themselves only at a late period, or even may not be produced at all.

The processes of exosmosis and endosmosis, therefore, in the living body, are regulated by the same or similar conditions as in artificial experiments; but they take place with greater rapidity, owing to the movement of the circulating blood, and the extent of contact existing between the bloodvessels and adjacent tissues. Although the arterial blood is everywhere the same in composition, yet its different ingredients are imbibed in varying quantities by the different tissues. And the proportion of each ingredient is determined, in each separate tissue, by its special absorbing or endosmotic power.

Albumen, under ordinary conditions, is not endosmotic; that is, it will not pass by transudation through an animal membrane. For this reason, the albumen of the blood, in the natural state of the circulation, is not exuded from the secreting surfaces, but is retained within the vascular system. But the degree of *pressure* to which a fluid is subjected has an influence in determining its endosmotic action. If the pressure upon the blood in the capillary vessels be increased, by obstruction to the venous current and backward congestion of the capillaries, then not only the saline and watery parts of the blood pass out in larger quantities, but the albumen itself may transude and infiltrate the neighboring parts. In this way albumen may make its appearance

in the urine, in consequence of obstruction to the renal circulation; and local œdema or general anasarca may follow upon venous congestion in particular regions, or upon general disturbance of the circulation.

The Lymph and Chyle.

The lymph is the fluid which, having been absorbed from the various tissues and organs of the body, is carried through the system of lymphatic vessels towards the centre of the circulation and is finally discharged, by the thoracic and right lymphatic ducts, into the great veins near the heart. As the chyle is simply the fluid of the mesenteric lymphatics, which assumes an opaque white color during digestion owing to the absorption of fat, it is properly studied at the same time with the lymph in general. The lymph has been obtained, for the purpose of examination, from the living animal, by introducing a silver canula of proper size into the thoracic duct at the root of the neck, or into large lymphatic trunks in other parts of the body. It was obtained by Rees from the lacteals of the mesentery and from the lymphatics of the leg in the ass, by Colin from the lacteals and thoracic duct of the ox, and from the lymphatics of the neck in the horse. We have obtained it from the thoracic duct both of the dog and the goat.

Physical Characters and Composition of the Lymph.—The lymph, thus obtained from the thoracic duct in the intervals of digestion, is an opalescent or nearly transparent, alkaline fluid, usually of a light amber color, and having a specific gravity of 1022. Its analysis shows a close resemblance in composition with the plasma of the blood. It contains water, fibrine, albumen, fatty matters, and the usual saline substances of the animal fluids. It is, however, decidedly poorer in albuminous ingredients than the blood. The following is an analysis by Lassaigne,[1] of the fluid obtained from the thoracic duct of the cow:

COMPOSITION OF THE LYMPH.

Water	964.0
Fibrine	0.9
Albumen	28.0
Fat	0.4
Sodium chloride	5.0
Sodium carbonate, Sodium phosphate, Sodium sulphate	1.2
Lime phosphate	0.5
	1000.0

Owing to the fibrine contained as an ingredient in the lymph, this fluid coagulates, like blood, within a few moments after its removal from the lymphatic vessels in the living animal, forming a gelatinous mass which

[1] In Colin, Physiologie comparée des Animaux domestiques. Paris, 1856, tome ii. p. 111.

is more or less colorless and transparent, or whitish and opaque, according to the proportion of fatty matter present in the specimen. After coagulation, it separates into a liquid serum and a solid clot, precisely as in the case of blood.

It thus appears that both fibrine and albumen are either formed in the interior of the lymphatic system, or transude to a certain extent from the bloodvessels, even in the ordinary condition of the circulation. If so, this transudation takes place in so small quantity that the albuminous matters are all taken up by the lymphatic vessels, and do not appear in the excreted fluids.

When lymph is drawn from the thoracic duct and allowed to coagulate, the clot after a few moments almost invariably assumes a decided pink color, and on microscopic examination is found to contain a very few red blood-globules. The presence of these globules is attributed by some competent authorities (Kölliker, Robin) to the accidental rupture of capillary bloodvessels and consequent introduction of their contents into the lymphatic system; but their occurrence is so constant that it must be doubted whether they have altogether an accidental origin. The pinkish color of the lymph under these circumstances is never perceptible when it is first drawn from the vessels, but only after it has been for a short time exposed to the air.

An important peculiarity in regard to the fluid of the lymphatic system, especially in the carnivorous animals, is that it varies, both in appearance and constitution, at different times. In the ruminating and graminivorous animals, as the sheep, ox, goat, and horse, it is either opalescent with a slight amber tinge, or nearly transparent and colorless. In the carnivorous animals, as the dog and cat, it is also opaline and amber colored in the intervals of digestion, but soon after feeding becomes of a dense, opaque, milky white, and continues to present that appearance until digestion and absorption are complete. It then regains its original aspect, and remains opaline until digestion is again in progress.

The results of analysis show that this variation in the appearance of the fluid of the thoracic duct during digestion, like that of the blood, is due to the absorption of fatty matters from the intestine. Although the chyle is richer than lymph in nearly all its solid ingredients, the principal difference between the two consists in the proportion of fat, which is nearly absent from the transparent or opaline lymph, but very abundant in the white and opaque chyle. This is shown in the following analysis by Dr. Rees,[1] of lymph and chyle from the ass.

[1] In Colin, Physiologie comparée des Animaux domestique. Paris, 1856 tome ii. p. 18.

COMPARATIVE ANALYSIS OF LYMPH AND CHYLE.

	Lymph.	Chyle.
Water	965.36	902.37
Albumen	12.00	35.16
Fibrine	1.20	3.70
Spirit extract	2.40	3.52
Water extract	13.19	12.33
Fat	traces	36.01
Saline matter	5.85	7.11
	1000.00	1000.00

When a canula, accordingly, is introduced into the thoracic duct at various periods after feeding, the fluid discharged varies considerably, both in appearance and quantity. In the dog, the fluid of the thoracic duct is never quite transparent, but retains a marked opaline tinge even so late as eighteen hours after feeding upon lean meat, and at least three days and a half after the introduction of fat food. Soon after feeding, it becomes whitish and opaque, and so remains while digestion and absorption are in progress. After the termination of this process it resumes its former appearance, becoming light colored and opalescent in the carnivorous animals, and nearly colorless and transparent in the herbivora.

The Lymph Globules.—The lymph, whatever may be its other ingredients, contains nearly always a greater or less abundance of rounded, transparent, or finely granular nucleated cells, similar to the white globules of the blood, which are known as the "lymph-globules." They vary in size from about 6 to 12 mmm. in diameter. By treatment with dilute acetic acid they become pale and transparent; while partial desiccation, or the contact of a concentrated saline or saccharine solution, gives them a shrivelled appearance with an irregular outline. According to the observations of Kölliker, the lymph-globules vary much, both in number and in size, according to the part of the lymphatic system from which the fluid is taken. In the smallest lymphatic vessels of the mesentery capable of examination, they may even be altogether absent, the lymph consisting of a perfectly homogeneous fluid, not holding any anatomical forms in suspension; and in the lymphatics where they first begin to show themselves, they are few in number and of less than the average size. After the lymph, however, has traversed one or two ranges of lymphatic glands, the globules are larger and more numerous, many of them in the larger lymphatic trunks attaining the size of 12 mmm. in diameter. From this circumstance, as well as from the microscopic texture of the glands themselves, it is concluded that the lymph-globules originate, in great part, in the interior of the lymphatic glands, and that they are brought thence by the current which traverses the lymph-paths in the substance of these organs.

Movement of the Fluids in the Lymphatic System.—The movement of the lymph in the lymphatic vessels differs from that of the blood, in the important particular that its course is always in one direction,

namely, from the periphery toward the centre. The fluids taken up by the lymphatic capillaries are collected into the larger branches and trunks, and by them conducted from without inward toward the heart.

The physical cause of the continuous movement of the lymph is primarily the *force of endosmosis* acting at the confines of the lymphatic system. As the volume of fluid accumulates in an endosmometer, in such a manner as to rise perceptibly in the upright tube, so the lymph accumulates by the force of absorption in the lymphatic capillaries, and thence fills the larger vessels of the system. It is evident that the pressure of fluids in a particular direction, due to the force of endosmosis, may be very considerable, since it is sometimes sufficient, as already shown, to burst the shell-membrane of a fowl's egg when placed in contact with water. As this pressure, in the lymphatic system, is always directed from without inward, and as the main lymphatic trunks finally terminate in the veins, the result is a uniform movement of the lymph, from the peripheral parts of the various organs and tissues toward the centre of the circulation.

The movement of the lymph is also aided by several secondary causes. As these vessels are provided with valves, even more abundantly than the veins, the alternate contraction and relaxation of the voluntary muscles in the limbs and trunk must facilitate considerably the passage of their fluids in an inward direction. The action of the heart and arteries also contributes indirectly to this result. As the thoracic duct passes upward through the chest, it crosses the median line obliquely from right to left, passing between the spinal column and the aorta; so that at each pulsation of the aorta it is compressed, and its contents urged toward its upper extremity. This effect is often very visible when a canula is inserted, in the living animal, into the thoracic duct at the root of the neck. Under these circumstances we have frequently seen the lymph projected from the extremity of the canula in a distinct jet at each cardiac pulsation, owing to the momentary pressure from the distended aorta.

Lastly, the thoracic movements of respiration take part in maintaining the flow of lymph. At each inspiration the resistance in the interior of the chest is diminished, and the lymph passes more readily from below into the thoracic duct; at each expiration the duct is subjected to compression, and is thus emptied of its fluids in a direction toward its junction with the veins. The influence of the respiratory movements, in a reversed form, may often be seen in animals poisoned by woorara, where artificial respiration is kept up through the trachea. If, in such an animal, a canula be inserted into the thoracic duct at the root of the neck, the flow of lymph from its open extremity is perceptibly increased at each forcible insufflation of the lung, since this produces more or less pressure upon the thoracic duct in the cavity of the chest.

Of these different physical causes of the lymph-current, the first alone, namely, the endosmotic action, is entirely uniform and continuous. The

others are all intermittent in their action, and depend for their efficiency upon the existence of valves in the lymphatic vessels. In a set of vessels provided with such valves, opening forward and shutting backward, any force which alternately compresses and releases them will necessarily cause the fluids which they contain to move in a definite direction. The mechanical forces above enumerated are more or less constantly active, and in point of fact exercise a considerable influence in producing an incessant transportation of the lymph from the periphery to the centre.

Total Daily Quantity of the Lymph and Chyle.—The quantity of fluids discharged from the thoracic duct within a given time varies according to the condition of abstinence or digestion. In the fasting condition it is comparatively moderate, but becomes more abundant soon after the commencement of digestion, to diminish again during the later stages of the process. We have found, at various periods after feeding, in the dog, the following quantities discharged per hour, for every thousand parts of the bodily weight of the animal:

Hourly Quantities of Lymph and Chyle in the Dog, per thousand parts of bodily weight.

3½ hours after feeding	2.45
7 " " "	2.20
13 " " "	0.99
18 " " "	1.15
18½ " " "	1.99

It would thus appear that the hourly quantity of these fluids, after diminishing during the latter stages of digestion, increases again somewhat about the eighteenth hour, though still considerably less abundant than while digestion is in active progress. It is probable that this increase at the two periods indicated is owing to two different causes. The fluid obtained in greatest abundance in the dog, in from 3 to 7 hours after feeding, is quite white and opaque, and its increase in quantity is evidently due to the admixture of chyle absorbed from the intestine. That obtained so late as the eighteenth hour is simply opaline, or more nearly transparent, and is composed of lymph alone. The absorption of chyle, therefore, takes place, of course, while digestion is in progress; but the most abundant production of lymph occurs some hours later, after the materials of nutrition have reached and permeated the tissues themselves.

The entire daily quantity of lymph and chyle is found, by direct observation, to be much larger than would be anticipated. In two experiments upon the horse, extending over a period of twelve hours each, Colin[1] obtained from the thoracic duct in this animal, on the average, 893 grammes of fluid per hour, which would amount to rather more than 20 kilogrammes per day. In the ruminating animals, according to the same observer, the quantity is still greater. In an ordinary

[1] Physiologie comparée des Animaux domestiques. Paris, 1856, tome ii. p. 106.

sized cow, the smallest quantity obtained, in an experiment extending over a period of twelve hours, was 625 grammes in fifteen minutes; that is, 2500 grammes per hour, or 60 kilogrammes per day. In another experiment with a young bull weighing 185 kilogrammes, he actually withdrew from the thoracic duct in the course of twenty-four hours, 15 kilogrammes of lymph and chyle, representing a little more than 8 per cent. of the entire bodily weight of the animal.

We have obtained similar results from experiments upon the dog and goat. In a young kid weighing 6.36 kilogrammes, we have obtained from the thoracic duct 122.5 grammes of lymph in three hours and a half. This quantity represents 35 grammes per hour, and, if continued throughout the day, would amount to 640 grammes, or fully 10 per cent. of the entire bodily weight. In the dog the fluids discharged from the thoracic duct are less abundant. The average of all the results obtained by us, in this animal, at different periods after feeding, gives very nearly four and a half per cent. of the bodily weight, as the total daily quantity of lymph and chyle. This is substantially the same result as that obtained by Colin in the horse; and for a man weighing 65 kilogrammes, it would be equivalent to about 3000 grammes of lymph and chyle per day. But this quantity represents both the products of lymphatic transudation and those of intestinal absorption taken together. An estimate of the total amount of the lymph alone must be based upon the quantity of fluids passing through the thoracic duct in the intervals of digestion, when no chyle is being taken up from the alimentary canal. In the dog, as shown by the experiments quoted above, the average quantity obtained, from the thirteenth to the eighteenth or nineteenth hour after feeding, when intestinal absorption had come to an end, was about 1.30 per thousand parts of the bodily weight; or, for the whole twenty-four hours, a little over 3 per cent. of the bodily weight. For a man of medium size, this would give not far from 2000 grammes as the average daily quantity of lymph alone.

Internal Renovation of the Animal Fluids.—By the combined actions of secretion, transudation, and reabsorption, a continual interchange or renovation of the animal fluids takes place in the living body, which is dependent for its materials upon the circulation of the blood, and which may be considered as a kind of secondary circulation through the substance of the tissues. For all the digestive fluids, as well as the bile discharged into the intestine, are reabsorbed in the natural process of digestion and again enter the current of the circulation. These fluids, therefore, pass and repass through the mucous membrane of the alimentary canal and adjacent glands, becoming more or less altered in constitution at each passage, but still serving to renovate alternately the constitution of the blood and the ingredients of the digestive secretions. The elements of the blood itself also transude in part from the capillary vessels, and are again taken up from the tissues by the lymphatics, to be finally restored to the venous blood, in the immediate neighborhood of the heart.

The daily quantity of all the fluids thus transuded and reabsorbed will serve to indicate the activity of endosmosis and exosmosis in the living body. In the following table, the quantities are all estimated, from preceding data, for a man of medium size.

TOTAL QUANTITY OF FLUIDS TRANSUDED AND REABSORBED DURING TWENTY-FOUR HOURS.

Saliva	1300	grammes.
Gastric juice	3000	"
Pancreatic juice	800	"
Bile	1000	"
Lymph	2000	"
	8100	

Not less than 8000 grammes therefore of the animal fluids, a quantity equal to that of the entire blood and amounting to more than 12 per cent. of the weight of the whole body, transude through the internal membranes and are restored to the blood by reabsorption, in the course of a single day. It is by this process that the natural constitution of the parts, though constantly changing, is still maintained in its normal condition, through the movement of the circulating fluids and the renovation of their materials.

CHAPTER XVII.

THE URINE.

THE urine is distinguished from all the other animal fluids by the fact that it represents only the products of the waste or physiological disintegration of the body. The living body, while in the active performance of its functions, is the seat of various manifestations of force, such as animal heat, sensibility, and motion, which are the indications of its vitality. These manifestations of force, in the living organism, as well as elsewhere, are only produced at the expense of its materials, and by their change of state or metamorphosis in the internal process of nutrition. It is accordingly an essential condition of the existence and activity of the animal body that it should go through with an incessant transformation and renewal of its component parts. Every living being absorbs more or less constantly certain nutritive materials from without, which are modified by assimilation and converted into the natural ingredients of its tissues. At the same time with this continuous process of growth and supply, there goes on an equally continuous change, by which the elements of the organized frame pass over into new forms of combination, destined to be expelled from the body as the products of its disintegration.

Certain substances, therefore, are constantly making their appearance in the animal tissues and fluids, which were not introduced with the food, but which have been produced in their interior by the process of continued metamorphosis. These substances result from the new combinations taking place in the organized frame. They are the forms under which those materials present themselves which have once made part of the animal tissues, but which have become altered by the incessant changes characteristic of living beings, and which are consequently no longer capable of exhibiting vital properties, or of aiding in the performance of the vital functions. The process of the elimination and removal of these materials is called *excretion*, and the materials themselves are known as the *excrementitious substances.*

These substances have peculiar characters by which they are distinguished from other ingredients of the living body. They are crystallizable and for the most part soluble in water, at least in the form under which they appear in the excreted fluids. They are formed in the blood or in the substance of the tissues from which they are absorbed by the blood, and are conveyed by the circulating fluid to the excretory organs through which they are discharged. If their elimination from the body be in any way arrested or impeded, their accumulation in the system produces a disturbance of the vital functions, which is more or

less severe according to their special character and the rapidity of their production. This poisonous influence is especially manifested in its action upon the nervous system, causing an abnormal irritability, derangement of the special senses, delirium, insensibility, coma, and death. These effects are more particularly marked in the case of urea after suppression of the urine; a complete stoppage of the elimination of this substance in the human subject usually producing a fatal result in three or four days.

The excrementitious matters, however, are not to be considered as poisonous, or even deleterious, in the quantities in which they normally occur in the animal solids and fluids. On the contrary, they are the natural products of the functional activity of the animal system, and are, therefore, as essential to the continued manifestation of life as the nutritious materials supplied by the food. It is only when the regular course of their elimination is retarded that they interfere with the due performance of the functions, by deranging the natural constitution of the tissues.

A variety of excrementitious substances are produced in the body, some of which are probably eliminated, in small proportion, with the perspiration or with the feces. The carbonic acid, exhaled in large quantity from the lungs, is to be regarded as belonging to this class, since it is produced in the substance of the tissues and constantly discharged by respiration. But the most important substances, usually included under the head of excrementitious matters, are distinguished by the fact that they contain nitrogen as one of their ultimate elements, and that they otherwise exhibit a remarkable analogy with each other in their chemical composition. They accordingly form a natural group of organic substances, resembling each other in their origin, their constitution, and their physiological destination. They are furthermore associated together by the circumstance that they are all eliminated from the body by the urine, of which they form the essential and characteristic ingredients.

The urine is therefore the only animal fluid which is solely an excretion. It is a solution of the nitrogenous excrementitious matters of the animal frame; and by its abundance and composition it indicates the activity of the healthy metamorphosis of the organic tissues and fluids. Beside its nitrogenous ingredients, it contains also most of the mineral salts which are discharged from the body; and by the water which holds these solid matters in solution it forms the channel for a large proportion of the fluids passing daily through the system. Furthermore, accidental or abnormal ingredients, introduced into the blood, almost invariably find their way out of the system by the kidneys, and thus appear as temporary ingredients of the urine. The constitution and physiological variations of this fluid during health, and its alteration in disease, are regulated by the corresponding changes of nutrition or activity in the body at large. The urine is therefore one of the most essential products of the animal system, and its formation is second in importance only to the function of respiration.

Physical Properties of the Urine.

The urine is a clear, amber-colored fluid, of a watery consistency, and with a distinctly acid reaction. As a general rule, its transparency is so nearly perfect that no appearance of turbidity is perceptible by ordinary diffused daylight. It contains, however, a very small quantity of mucus from the urinary bladder, which may be rendered visible as a faint opalescence when a sunbeam is made to pass through it in a lateral direction. If the urine be allowed to remain at rest for a few hours in a cylindrical glass vessel, the mucus gradually subsides, forming a very light cloudy mass at the bottom and leaving the supernatant fluid entirely clear. The ingredients of the urine itself are all therefore in a state of complete solution. While still warm and fresh, the urine has a peculiar but not offensive odor, which disappears on cooling and may be then restored by gentle heating. The average specific gravity of healthy urine, in the adult, is from 1020 to 1025; and its daily quantity is about 1200 cubic centimetres.

Variations of the Urine in Quantity, Acidity, and Specific Gravity.—The urine does not present uniformly the same characters, but varies normally from hour to hour, in each individual, at different periods of the day. It is usually discharged from the bladder five or six times in the twenty-four hours, and each specimen shows more or less variation in its physical properties. This variation depends upon the changing conditions of the body, as to rest, exercise, food, drink, sleeping, and waking. In the same person, leading a uniform mode of life from day to day, the diurnal variations of the urine follow each other with great regularity; although in different persons, whose habits are different, they may not be altogether the same. As a general rule, the urine which collects in the bladder during the night and is first discharged in the morning is strongly colored, of high specific gravity, and has a very distinct acid reaction. That passed during the forenoon, on the other hand, is pale and of comparatively low specific gravity; often falling so low as 1018 or even 1015. At the same time, its acidity diminishes or even disappears altogether; so that at this time in the day the urine is frequently neutral or slightly alkaline. Toward noon, its density and depth of color increase, and its acidity returns. All these properties become more strongly marked during the afternoon and evening; and toward night the urine is again deeply colored and strongly acid, and has a specific gravity of 1028 or 1030.

The following instances will serve to show the general characters of this variation:

Observation First. *March 20th.*

Urine of	1st	discharge,	acid,	sp. gr.	1025.
"	2d	"	alkaline,	"	1015.
"	3d	"	neutral,	"	1018.
"	4th	"	acid,	"	1018.
"	5th	"	acid,	"	1027

OBSERVATION SECOND. *March* 21*st.*

Urine of 1st	discharge,	acid,	sp. gr.	1029.
" 2d	"	neutral,	"	1022.
" 3d	"	neutral,	"	1025.
" 4th	"	acid,	"	1027.
" 5th	"	acid,	"	1030.

These variations do not always follow a perfectly regular course, since they are liable to temporary modification from accidental causes during the day; but their general tendency corresponds with that given above.

The acidity of the urine is also liable to vary from temporary causes, owing to the introduction of organic substances with the food which give rise to alkalescence in the animal fluids. The salts of the organic acids, such as the *lactates*, *acetates*, *malates*, and *tartrates*, when taken into the stomach and absorbed by the circulation, are replaced by carbonates of the same bases, and appear under that form in the urine. When these salts, or the fruits and vegetables which contain them, are taken in large quantity, the urine becomes alkaline from the presence of the carbonates. The use of summer fruits, therefore, though they may have an acidulous taste, is followed by alkalescence of the urine. The effect thus produced may be manifested in a very short time; according to the observations of Lehmann, the urine sometimes becoming alkaline within a quarter of an hour after taking a little over 15 grammes of sodium acetate.

It is evident, therefore, that when the specific gravity or the acidity of the urine is to be tested, either in health or disease, it will not be sufficient to rely upon the examination of a single specimen. The normal variations in specific gravity during the day do not usually exceed the limits of 1015 as a minimum and 1030 as a maximum; but either of these would be unnatural if continued during the whole twenty-four hours. All the different specimens of urine passed during the day should therefore be collected and examined together. The average specific gravity thus obtained will represent the normal daily density of the excretion.

The daily volume of the urine is also to be taken into account. The total amount of solids discharged by the urine in health is from 50 to 60 grammes per day; and this quantity of solid material is dissolved in about 1200 cubic centimetres of water. This gives an average daily quantity and an average specific gravity of the urine, as the measure of the excretory process during twenty-four hours.

Both the quantity of the urine and its mean specific gravity are liable to vary somewhat in different individuals, or even in the same individual from day to day. Ordinarily, the water of the urine is more than sufficient to hold all the solid matters in solution; and its proportion may therefore be diminished by temporary causes without the production of turbidity or the formation of a deposit. Under such circumstances, the urine merely becomes deeper in color, and of higher

specific gravity. If a smaller quantity of water than usual be taken into the system with the drink, or if the exhalation from the lungs and skin, or the intestinal discharges, be increased, a smaller quantity of water will necessarily pass off by the kidneys; and the urine will be diminished in quantity, while its specific gravity is increased. The urine is sometimes reduced in this way to 500 or 600 cubic centimetres per day, its specific gravity rising at the same time to 1030. On the other hand, if the fluid ingesta be unusually abundant, or if the perspiration be diminished, the surplus quantity of water will pass off by the kidneys; so that the amount of urine in twenty-four hours may be increased to 1350 or 1400 cubic centimetres, and its mean specific gravity reduced at the same time to 1020 or even 1017. Under such conditions, the total amount of solid matter discharged remains about the same. These changes depend simply upon the fluctuating quantity of water, which may pass off by the kidneys in larger or smaller quantity, according to circumstances. In purely normal or physiological variations of this nature, the entire quantity of the urine and its mean specific gravity vary always in an inverse direction with regard to each other; the former increasing while the latter diminishes, and *vice versâ.* If, however, it be found that both the quantity and specific gravity of the urine are increased or diminished at the same time, or if either one be increased or diminished while the other remains stationary, such an alteration will show an actual change in the total amount of solid ingredients, and consequently an unnatural and pathological condition.

Ingredients of the Urine.

The chemical composition of the urine, as derived from the most recent and numerous analyses, is as follows:

Composition of the Urine.

	Water	950.00
Nitrogenous organic substances.	Urea	26.20
	Creatinine	0.87
	Sodium and potassium urates	1.45
	Sodium and potassium hippurates	0.70
Mineral salts.	Sodium biphosphate	0.40
	Sodium and potassium phosphates	3.35
	Lime and magnesium phosphates	0.83
	Sodium and potassium chlorides	12.55
	Sodium and potassium sulphates	3.30
	Mucus and coloring matter	0.35
		1000.00

The constitution of the urine is not invariable, but changes more or less at different periods of the day, according to the rapidity of excretion of its different ingredients. The foregoing list, however, represents, in an approximate manner, its average composition for the entire twenty-four hours.

Urea.—This is the most important constituent of the urine, both in regard to character and amount, forming more than one-half the entire quantity of its solid ingredients, and over 80 per cent. of all those of an organic nature. The most important fact known with regard to the origin of urea is, that it is not formed in the kidneys, but pre-exists in the blood in small proportion, and is drained away from the circulating fluid during its passage through the renal vessels. This was first shown by the experiments of Prevost and Dumas,[1] who, after extirpating the kidneys, or tying the renal arteries in the living animal, found the quantity of urea in the blood increased in marked proportion, owing to the arrest of its elimination by the kidneys. It has also been found in the blood of the human subject in cases of renal disease, sometimes in so large a proportion as 1.5 parts per thousand,[2] or nearly ten times its normal quantity. It has not been found, however, in sufficient quantity in any of the solid tissues to indicate the immediate source of its production. It is either formed in the blood itself, by transformation of some previous nitrogenous combination, or it is absorbed by the blood too rapidly to be detected as an ingredient of the solid tissues.

Urea is obtained most readily from the urine by first converting it into the form of a nitrate. For this purpose the fresh urine is evaporated over the water-bath until it is reduced to one-quarter of its original volume. It is then filtered, and the filtered fluid mixed with an equal quantity of nitric acid, which produces nitrate of urea. This salt, being less soluble than urea, rapidly separates in the form of abundant crystalline scales. The crystalline deposit is separated from the mother liquor, mixed with water, and decomposed by the addition of barium carbonate, which sets free the urea, with the formation of barium nitrate. This process is continued so long as carbonic acid is given off; after which the whole is evaporated to dryness, and the dry residue extracted with absolute alcohol, which dissolves out the urea. The alcoholic solution is then filtered and evaporated until the urea separates in a crystalline form.[3]

The *quantity* of urea in a given volume of urine is readily ascertained by decomposing it, according to Davy's method, with a solution of sodium hypochlorite. A long and narrow graduated glass tube, open at one extremity, and capable of holding about 50 cubic centimetres of fluid, is filled to a little more than one-third its capacity with mercury, upon which are poured 3 or 4 cubic centimetres of the urine to be ex-

[1] Prevost and Dumas, Annales de Chimie et de Physique, 1823, tome xxiii. p. 90; Ségalas, Journal de Physiologie, tome ii. p. 354; Mitscherlich, Tiedemann, and Gmelin, Poggendorf's Annalen, band xxxi. p. 303; Cl. Bernard, Liquides de l'Organisme. Paris, 1859, tome ii., Deuxième Leçon.

[2] In Milne Edwards, Leçons sur la Physiologie. Paris, 1857, tome i. p. 298.

[3] Hoppe-Seyler, Handbuch der Physiologisch- und Pathologisch-Chemischen Analyse. Berlin, 1870, p. 120.

amined. The remainder of the tube is then filled with the sodium hypochlorite solution, the mouth of the tube closed, the fluids well mixed, and the tube then inverted in a shallow glass dish filled with a saturated solution of sodium chloride. The mixture of urine and hypochlorite solution remains in the tube; and as the urea is decomposed, its nitrogen is given off in the gaseous form and collects in the upper closed end of the tube, where its volume may be read off on the scale, after the action has ceased. Every cubic centimetre of nitrogen, thus disengaged, represents 2.5 milligrammes of urea.

The conditions influencing the quantity of urea produced and discharged in the healthy subject during twenty-four hours, are the size and general development of the body, the nature of the food, and the state of rest or activity. Like other products of the living organism, its quantity is in proportion to the entire mass of the body. As a general rule, its daily quantity, in man, is 0.5 per thousand parts of the entire bodily weight; and for a man of medium size it amounts to about 35 grammes per day. As it is a nitrogenous substance, resulting from the final consumption of the albuminous elements of the system, its proportion is greater under a diet of animal food, which is comparatively rich in albuminous matters, than under one of vegetable food, in which these substances are less abundant. Its daily quantity falls to a minimum when the diet is exclusively confined to non-nitrogenous articles of food, namely, starch, sugar, and fat. It is still, however, produced and excreted under an exclusively non-nitrogenous diet, and even when no food whatever is taken, so long as the animal functions continue to be performed.

The results obtained by nearly all experimenters led to the conclusion that the quantity of urea excreted is especially increased by *muscular exertion*, until a doubt was thrown upon this point by Fick and Wislicenus in 1866. These observers ascended a mountain on foot, the ascent occupying a little over eight hours; during which time, and for seventeen hours beforehand, they confined themselves to a diet of non-nitrogenous food. They found the amount of urea discharged per hour to be less, while engaged in ascending the mountain, than it was before; but it increased during the following night, after a meal of animal food.

Subsequent observers have obtained various results. Dr. Parkes, in a series of very careful and extended observations,[1] found that the discharge of urea was increased not during, but after, a period of muscular work. This was shown even in a man confined for five days to a non-nitrogenous diet, in whom the discharge of urea was not increased on the day of unusual muscular effort, but on the following day was a little more than doubled.

The observations of Prof. A. Flint, Jr., on the excretion of urea in the case of the pedestrian Weston, have the important advantage of ex-

[1] Proceedings of the Royal Society of London, vol. xvi. p. 48, and March 2, 1871.

tending over comparatively long periods, both of exercise and rest, the diet at the same time remaining unchanged in its general characters.

The pedestrian was under observation for fifteen days; namely, five days previous to the walk, five days during its continuance, and five days immediately afterward. For the period preceding the walk, the average exercise was about eight miles per day; during the walk it was nearly sixty-four miles per day, and for the period subsequent to the walk, it was a little over two miles per day. The results obtained during the three periods showed, accordingly, the normal amount of urea excreted by the pedestrian under ordinary conditions, the amount discharged during an unusual and nearly continuous muscular exertion, and the subsequent effects of the exertion on the general condition of the system.

The nitrogenous ingredients of the food, during all three periods, were also recorded, so that the influence of the food itself on the amount of urea may be estimated at the same time with that of the muscular exertion.

The following table gives the main result of these experiments, so far as they are connected with the present subject:

Daily Quantity of	First Period. Five days before the walk.	Second Period. Five days during the walk.	Third Period. Five days after the walk.
Urea	628.24 grains.	722.16 grains.	726.79 grains.
Nitrogen in food . . .	339.46 "	234.76 "	440.93 "
Nitrogen in urea . . .	293.18 "	337.01 "	339.17 "
Total nitrogen in urea and feces	315.09 "	361.52 "	373.15 "
Nitrogen in urea and feces per 100 parts of nitrogen in food	95.53	174.81	91.93

It is evident, therefore, that during the time of unusual muscular exertion the daily quantity of urea was increased by nearly fifteen per cent. over that of the previous ordinary condition, the nitrogenous elements of the food being at the same time considerably diminished; and that, during the period of exertion, the total quantity of nitrogen discharged by the urea and feces combined was nearly seventy-five per cent. greater than that introduced with the food, while in both the previous and subsequent periods it was from about four and a half to eight per cent. less. During the period of exertion there was a loss of nearly three and a half pounds of bodily weight, and an increase of similar amount during the subsequent period of rest. The author fairly explains the above loss of weight by the disintegration of muscular tissue; and the subsequent increase, by a retention of nitrogenous constituents in the body, to repair the waste thus produced.

"During the five days of the walk,[1] Mr. Weston consumed in all 1173.80 grains of nitrogen in his food. During the same period he

[1] New York Medical Journal, June, 1871, p. 669.

eliminated 1807.60 grains of nitrogen, in the urine and feces. This leaves 633.80 grains of nitrogen, over and above the nitrogen of the food, which must be attributed to the waste of his tissues, and probably almost exclusively to the waste of his muscular tissue. According to the best authorities, lean meat uncooked, or muscular tissue, contains 3 per cent. of nitrogen. The loss of 633.80 grains of nitrogen would then represent a loss of 21,127.00 grains, or 3.018 lbs. of muscular tissue. The actual loss of weight was 3.450 lbs. This allows about 0.43 lb. of loss unaccounted for, which might be fat or water."

Creatinine.—This substance is perhaps next in physiological importance to the urea, considering its analogy in chemical composition, but is produced in much smaller quantity; its total amount usually not exceeding 1 gramme per day. It has not been found in any of the solid tissues; but it is probably derived by transformation of the creatine of the muscles, since it may be artificially produced from the latter by the action of heat and dilute sulphuric acid. It is undoubtedly, like urea, a product of the metamorphosis of the albuminous ingredients of the body, from which it derives its nitrogenous element. But little is known with regard to the conditions which increase or diminish its production.

Sodium and Potassium Urates.—The urates are due to a combination of the alkaline base with a nitrogenous mineral acid, belonging to the same physiological class of excrementitious matters as urea and creatinine. This substance is known to be, like urea, increased in quantity by a nitrogenous, and decreased by a non-nitrogenous diet; but its relations to muscular exercise and other temporary conditions are not fully known. The urates are readily soluble in water, and are usually excreted to the amount of about 1.75 gramme per day. The *hippurates* have, in general, similar chemical and physiological relations to those of the urates, excepting that they are more abundant under the use of a vegetable diet, and disappear altogether when the food is exclusively of an animal nature. In the human subject under an ordinary mixed diet, they amount to about one-half the quantity of the urates.

The preceding ingredients of the urine are all associated in a single physiological group, forming its nitrogenous excrementitious substances. Beside them, it also contains a variety of inorganic or mineral constituents, derived from the waste of the animal tissues and fluids.

Acid Sodium Phosphate, or sodium biphosphate.—This is the ingredient which gives to the urine its acid reaction to test-paper. It is regarded as derived from the ordinary sodium phosphate of the blood ($Na_2H\ PO_4$) by the action of the uric acid produced in the system, which unites with a part of its sodium, forming sodium urate, and leaving an acid sodium phosphate (NaH_2PO_4). The uric acid produced from the decomposition of animal substances, although it does not itself appear in a free form, is, therefore, indirectly the cause of the acid reaction of the urine; and this reaction will vary in intensity with the amount of uric acid discharged.

The Alkaline Phosphates, or ordinary phosphates of sodium and potassium.—These are the soluble phosphates, which exist in the blood as well as in the urine, and which, in solution, have a mild alkaline reaction. Owing to their ready solubility, they never appear as a precipitate, nor disturb in any way the transparency of the urine. It is under the form of these salts that most of the phosphoric acid in combination is discharged with the urine. According to Vogel, the excretion of phosphoric acid by this channel is increased by the use of food containing soluble phosphates or substances capable of yielding phosphoric acid by the changes which they undergo in the system. It is accordingly more abundant under a diet of animal food, less so under a vegetable regimen. Its discharge, however, does not depend exclusively upon the ingredients of the daily food, since it continues, although in diminished quantity, after long-continued abstinence from all food. Its immediate origin is, therefore, wholly or partly from the constituents of the body itself. The observations of Wood,[1] as well as those of Vogel and others, show also that there is a diurnal variation of considerable regularity in the normal excretion of the salts of phosphoric acid. Its hourly quantity is at a minimum during the forenoon, increases in the latter part of the day after the principal meal, and reaches a maximum in the evening or during the night, to diminish again on the morning of the following day. It is under the form of phosphates that the phosphorus contained in certain organic substances (lecithine) is finally discharged from the system. The average quantity of the alkaline phosphates discharged during health under an ordinary diet is a little over four grammes per day.

The Earthy Phosphates, or the phosphates of lime and magnesium.—The earthy phosphates are usually present in the urine in much smaller quantity than the preceding. They are held in solution only by the acid reaction of the urine, and when this is absent or very much diminished they are thrown down as a light precipitate, consequently, the neutral or faintly alkaline urine passed in the forenoon is often slightly turbid with a deposit of the earthy phosphates, without, however, indicating any abnormal increase in their amount. According to the extensive and careful observations of Wood, the alkaline and earthy phosphates differ from each other in the conditions which influence their excretion. While the alkaline phosphates of the urine are increased in amount during continued mental application, the earthy phosphates are diminished, and the total quantity of both kinds is not materially altered. The earthy phosphates, on the other hand, are increased by abstinence from mental labor. Their average daily quantity under ordinary conditions is about one gramme, or rather less than one-quarter that of the earthy phosphates.

[1] On the Influence of Mental Activity on the Excretion of Phosphoric Acid by the Kidneys. Proceedings of the Connecticut Medical Society, 1869.

Sodium and Potassium Chlorides.—The sodium chloride, which represents nearly the whole of these two salts, is also by far the most abundant mineral ingredient in the urine, forming over one-half of its inorganic constituents. It is derived in great measure from the sodium chloride taken with the food, and is increased or diminished in quantity with the variation in the amount of common salt in the diet. Various circumstances, however, influence its excretion at different periods of the day. Its hourly discharge is habitually least during the night, increases in the forenoon and is greatest during the latter part of the day. According to Vogel,[1] both mental and bodily exertion perceptibly increase its excretion; and even water, when taken in unusual abundance, by increasing the activity of the kidneys, causes also a temporary augmentation in the discharge of sodium chloride, which is subsequently followed by a corresponding diminution. The average amount of the chlorides discharged with the urine is about fifteen grammes per day.

Sodium and Potassium Sulphates.—The sulphates present in the urine are derived partly from those which have been introduced, under their own form, as ingredients of the food; and observation has shown that their quantity is increased by the medicinal administration of sulphuric acid or of sodium sulphate. The administration of sulphur or the sulphurets produces a similar effect. The albuminous matters of the system, furthermore, which contain sulphur as one of their constituent elements, give rise, by their changes in the oxidizing process of nutrition and excretion, to sulphuric acid and the sulphates; since the whole of their carbon, hydrogen, and nitrogen is finally discharged under the form of water, carbonic acid, and urea, while the small quantity of sulphur remaining appears as sulphuric acid in the sulphates. Consequently the excretion of sulphates, as shown by Vogel, is increased by an abundant diet of animal food, and diminished under a vegetable regimen. The sulphates are freely soluble and never appear as a spontaneous precipitate in the urine. Their average quantity is about 3.96 grammes per day.

Reactions of the Urine to Chemical Tests.

The reactions of the urine to a variety of ordinary tests form a ready criterion for ascertaining its normal or abnormal constitution. The more exact quantitative determination of its ingredients requires the attention and skill of the professional chemist; but many of its important characters may be recognized by the use of simple means.

The Application of Heat.—If transparent healthy urine, of a distinctly acid reaction, be heated in a test-tube over a spirit lamp to the boiling point, no change in its appearance is produced. If its acidity be very slightly pronounced, on the other hand, it becomes turbid on boiling, from a precipitation of its earthy phosphates. This is because the earthy phosphates are less soluble in a hot than in a cold liquid;

[1] Analyse des Harns. Wiesbaden, 1872, p. 350.

and the faintly acid reaction of the urine, which was enough to hold them in solution at ordinary temperatures, is no longer sufficient after the application of heat, and the phosphates are accordingly thrown down as a deposit. The precipitation from this cause is never very abundant, and it is instantly cleared up again by the addition of a drop of nitric acid, which restores the normal acidity of the urine. The turbidity thus produced by boiling, from the precipitation of the earthy phosphates, is not, therefore, usually due to an increased quantity of these salts in the urine, but simply to a deficiency of its acid reaction.

Diseased urine may also become turbid on boiling, from the coagulation of *albumen.* This is readily distinguished from a precipitation of the earthy phosphates by two facts—namely, first, that it may take place in urine which is distinctly acid; and second, that the addition of nitric acid, which redissolves the phosphatic precipitate, only increases the turbidity which is due to albumen.

Acids.—The addition of the mineral acids to healthy urine produces no immediate visible effect, beyond increasing its acidity and slightly modifying its color. They, however, decompose its urates; and the uric acid thus set free is slowly deposited in the crystalline form. If nitric or hydrochloric acid be added to fresh filtered urine, in the proportion of about 2 per cent. by volume, and the mixture be allowed to remain at rest for twenty-four or forty-eight hours, the sides and bottom of the vessel become covered with a thinly scattered deposit of uric acid crystals. These crystals have usually the form of transparent rhomboidal plates, or oval laminæ with pointed extremities, and are generally tinged of a yellowish hue by the coloring matter of the urine. They are frequently arranged in radiated clusters, or small spheroidal masses, presenting the appearance of minute calculous concretions, which vary much in size and regularity, according to the time occupied in their formation.

Fig. 129.

CRYSTALS OF URIC ACID; deposited from urine, after the addition of nitric acid.

The deposit of uric acid crystals, thus formed in healthy urine from the addition of a mineral acid, is always scanty in amount, and only becomes visible as a crystalline precipitate after several hours.

In rare cases, when the urine is loaded with an unusual proportion of the urates, a few drops of nitric acid will produce at once a perceptible turbidity, from the precipitation of abundant microscopic crys-

tals of uric acid. This deposit may be distinguished from albumen by the appearance of the crystals under the microscope, and also by the fact that, unlike albumen, it is not produced by the application of a boiling temperature.

When the urine is scanty and concentrated, owing to temporary causes, with a specific gravity of 1030 to 1035, but without any abnormal ingredient, if it be mixed with one-half its volume of nitric acid and exposed to a low temperature, a crystallization of nitrate of urea will often take place in the course of half an hour or an hour. This is due simply to the diminished proportion of water, which is still sufficient to hold the urea in solution, but allows a separation of nitrate of urea when this salt is formed by the addition of nitric acid. It never takes place when the urine has its normal specific gravity of 1020 to 1025.

Alkalies.—The addition of a free alkali or an alkaline carbonate to normal urine diminishes its acid reaction, and, as soon as the point of saturation has been reached, produces a turbidity, owing to the precipitation of the earthy phosphates. These are the only ingredients of the urine which are thrown down by the addition of an alkali, and a free acid immediately restores its transparency.

Mineral Salts.—Solutions of barium chloride, barium nitrate, or the tribasic lead acetate, when added to healthy urine, decompose its sulphates, and produce a dense precipitate of the corresponding metallic salts. Solutions of silver nitrate produce a precipitate with the sodium and potassium chlorides, forming silver chloride which is insoluble. The tribasic lead acetate and silver nitrate also throw down mucus and coloring matters.

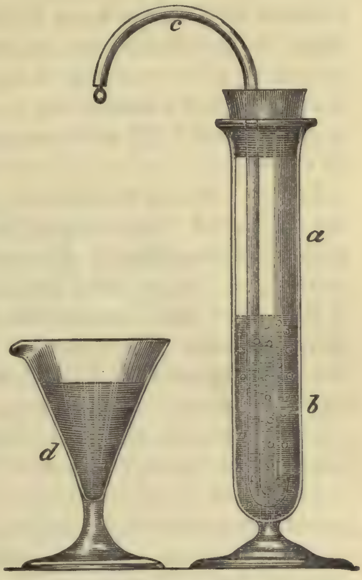
Abnormal Ingredients of the Urine.

The abnormal ingredients which appear in the urine are either: 1st. Foreign substances accidentally present in the blood, which are eliminated by the kidneys, such as glucose, biliary matters, and medicinal substances; or 2d. The albuminous constituents of the blood, which are discharged with the urine owing to a disturbance of the renal circulation.

Glucose.—The presence of glucose in the urine is characteristic of diabetes mellitus. In this disease the urine is generally increased in quantity and at the same time of unusually high specific gravity, namely, from 1035 to 1050. It is of a light, clear, amber or straw color, and remarkably transparent; so that it has the appearance of being dilute, although it is in reality denser than usual, owing to the presence of glucose in solution. The glucose is detected by the application of Trommer's or Fehling's test, or by that of fermentation. For the latter purpose a little yeast should be mixed with 15 or 20 times its volume of water, and the mixture allowed to remain at rest in a cylindrical upright glass vessel until the yeast globules have subsided in a dense homogeneous layer at the bottom. The supernatant fluid, containing the

soluble impurities of the yeast, is poured off, and a small quantity of the moist yeast-deposit at the bottom is added to the urine under examination. The mixture is then placed in a ferment-apparatus and kept at a temperature of about 25° (77° F.), for forty-eight hours, when the gaseous products of fermentation will have been completely disengaged. The most convenient form of apparatus is a test-tube of known capacity (Fig. 130, *a*, *b*), supported by a foot and provided with an India-rubber stopper, through which passes a narrow glass tube (*c*), open at both ends; its inner portion reaching to the bottom of the test-tube, where it is bent upward, to prevent the escape of gas, its outer portion being bent downward, to allow the liquid expelled to drop freely from its orifice. The test-tube may be graduated in cubic centimetres from above downward. The apparatus being filled with saccharine urine, when fermentation begins the disengaged gas rises in bubbles to the upper part of the test-tube and collects there, while the urine is forced out through the bent glass tube. Every cubic centimetre of carbonic acid produced corresponds to 0.26 milligrammes of sugar decomposed. A similar apparatus, containing the same quantity of healthy urine and yeast, should be kept at the same temperature for an equal time, as a comparative test; since a small quantity of carbonic acid might be disengaged from the yeast itself, owing to its imperfect purification. The difference between the two cases is that in the yeast alone the disengagement of gas soon ceases; while in a saccharine solution the yeast-cells multiply indefinitely, and carbonic acid continues to be produced until most of the sugar has been decomposed. This method does not give the precise quantity of the glucose contained in any single specimen, since some of the urine escapes before its fermentation is fully completed; but it is at the same time the surest indication of the existence of sugar, and a ready means of determining approximatively whether it be scanty or abundant in amount.

Fig. 130.



FERMENT-APPARATUS, containing saccharine urine in fermentation.—*a.* Upper part of the test-tube containing carbonic acid. *b.* Lower part of the test-tube containing the fermenting liquid. *c.* Bent glass tube, to allow the escape of liquid. *d.* Liquid which has been forced out from the test-tube by the accumulation of gas.

The simplest method of ascertaining the quantity of glucose in a given specimen of urine with sufficient accuracy for all clinical pur-

poses is that of Dr. Roberts,[1] which depends upon the loss of specific gravity occasioned by the decomposition of the glucose in fermentation. A portion of the urine is taken and its specific gravity ascertained at the temperature of 25° (77° F.). A little yeast is then added and the mixture kept at the same temperature until fermentation has ceased; when the specific gravity is again taken. The diminution in density caused by the conversion of the glucose into alcohol and carbonic acid is such that the loss of one degree in specific gravity indicates the disappearance of 2.197 milligrammes of glucose for every cubic centimetre of urine.

The glucose can be obtained directly from diabetic urine, according to the method of Hoppe-Seyler, by evaporating the urine over the water-bath to the consistency of a syrup, and allowing it to remain at rest for some days or weeks until completely crystallized. The crystalline mass is triturated and washed with a small quantity of cold alcohol, to remove the urea. The residue is then extracted with boiling alcohol, and the alcoholic solution filtered while still hot, after which the glucose is deposited in a crystalline form.

The glucose of diabetic urine is not formed in the kidneys, but pre-exists in the blood, from which it is eliminated in the renal circulation. If a solution of sugar be introduced in sufficient quantity directly into the bloodvessels of the rabbit, or injected into the subcutaneous connective tissue so as to be absorbed thence by the blood, it is soon discharged by the kidneys. It has been shown by Bernard,[2] that the time within which sugar appears in the urine under these circumstances varies with the quantity injected and the rapidity of its absorption. If a solution of one gramme of glucose in 25 cubic centimetres of water be injected under the skin of a rabbit weighing a little over one kilogramme, it is entirely destroyed in the circulation, and does not pass out with the urine. A dose of 1.5 gramme, however, injected in the same way, appears in the urine at the end of two hours, 2 grammes in an hour and a half, 2.5 grammes in an hour, and 12.5 grammes in fifteen minutes. Whenever, accordingly, glucose accumulates in the circulation beyond a certain quantity in proportion to the whole mass of the blood, it is eliminated as a foreign substance, and appears as an ingredient of the urine.

Biliary Matters.—In some cases of jaundice, the coloring matter of the bile passes into the urine in sufficient abundance to give to the fluid a deep yellow or yellowish-brown tinge, so that it may even stain linen or cotton fabrics, with which it comes in contact, of a similar color. The saline biliary substances, namely, sodium glycocholate and taurocholate, according to Lehmann, have also been detected in the urine. In these instances, the biliary matters are reabsorbed from the hepatic ducts and conveyed by the blood to the kidneys.

[1] Urinary and Renal Diseases. Philadelphia edition, 1872, p. 198.
[2] Leçons de Physiologie Expérimentale. Glycogénie. Paris, 1855, p. 216.

Potassium ferrocyanide, when introduced into the circulation, appears with great readiness in the urine; and, according to the observations of Bernard, may begin to be eliminated within twenty minutes after being injected into the duct of the submaxillary gland.

Iodine, in all its combinations, passes out by the same channel. After the administration, in the healthy human subject, of 192 milligrammes of iodine, in the form of syrup of the iodide of iron, we have found it to be present in the urine at the end of thirty minutes, and that it continued to be discharged for nearly twenty-four hours. In the case of two patients who had been taking potassium iodide, one of them for six weeks, the other for two months, the urine still contained iodine at the end of three days after the suspension of the medicine; but at the end of three days and a half it was no longer present. Even when iodine, however, is taken in a free form, as in that of alcoholic solution, it always passes out by the urine in combination. It cannot be detected, accordingly, by the simple admixture of starch with the urine, but must be set free by the addition of a drop or two of nitric acid, after which it produces its characteristic blue color by union with the starch. The same thing is true of the other animal fluids, such as the saliva and the perspiration, by which iodine is also eliminated after its introduction into the system.

Quinine, when taken as a remedy, has been detected in the urine. *Ether* passes out of the circulation in the same way, and its odor may sometimes be very perceptible in the urine, after having been inhaled for the purpose of producing anæsthesia. The peculiar odors developed in the urine after the use of *Asparagus*, and certain other vegetable substances, are produced by a transformation of their ingredients while passing through the animal system.

Albumen.—Under ordinary conditions the albumen of the blood does not pass out in any proportion from the renal vessels; but whenever the pressure in these vessels is increased beyond a certain point, owing to congestion, compression of the renal veins by abdominal tumors, pregnancy, or altered nutrition of the kidneys in Bright's disease, the albuminous ingredients of the blood transude through the capillaries and make their appearance in the urine.

Albuminous urine is usually rather pale, and often somewhat opalescent from the admixture of exfoliated epithelium cells or of fibrinous casts from the uriniferous tubules of the kidney. When this is the case, it should be rendered transparent by filtration before applying the tests, since the turbidity already existing might mask the reaction, if the albumen were present in small proportion.

If the urine have an acid reaction, the application of heat produces a turbidity which is more marked in proportion to the quantity of albumen which it contains. In extreme cases the fluid may solidify, like the serum of blood, before reaching the boiling point; but the albumen is more frequently thrown down in loose whitish flakes. When the

turbidity produced by boiling is moderate in amount, it may resemble that due to the precipitation of the earthy phosphates. It can, however, be distinguished by the addition of a drop of free acid, which at once redissolves the earthy phosphates, while it does not affect a turbidity caused by albumen. An albuminous precipitate, on the contrary, however abundant, is redissolved by the addition of a caustic alkali.

If the urine be alkaline in reaction, boiling may not throw down the albumen present, this substance being soluble in an alkali. Urine, accordingly, which is suspected of being albuminous, should be first rendered distinctly acid in reaction, if necessary, by the addition of a small quantity of acetic acid.

Nitric acid, added to albuminous urine, produces a turbidity by coagulation of the albumen. Alcohol, added to the urine in equal volume, will have the same effect; and a solution of potassium ferrocyanide, acidulated with acetic acid, will also produce coagulation. All the above tests, if applied in succession, will leave no doubt as to the presence or absence of albumen.

Deposits in the Urine.

The deposits which appear spontaneously in the urine consist either: 1st, of some of its normal ingredients, thrown down in consequence of a disturbance in its relative composition; or 2d, of exudations from the mucous membrane of the urinary passages, owing to a diseased condition of the parts. Those belonging to the first class are the earthy phosphates and the urates. The most common of those belonging to the second are blood, mucus, and pus.

Deposits of the Earthy Phosphates.—These deposits are always of a white color, and are seldom abundant. When the urine is first passed, the phosphates are disseminated through its mass in the form of a light cloudiness, which settles slowly to the bottom of the vessel. The urine is alkaline or neutral in reaction, and is usually of less than the average specific gravity. The precipitate is amorphous, presenting no crystalline forms under the microscope. It is at once redissolved on the addition of an acid, and presents all the chemical reactions which have been described as belonging to the earthy phosphates. The alkaline reaction of the urine, which gives rise to the appearance of this deposit, may be due to a temporary diminution in the quantity of uric acid produced in the system, or to an unusual formation of alkaline carbonates from the use of fruits or vegetables containing salts of the vegetable acids.

Deposits of the Urates.—The urates appear as a deposit when the formation of uric acid in the system is unusually abundant in proportion to the entire quantity of the urine, so that a portion of the urates are no longer held in solution. The urine is nearly always concentrated, highly colored, above the average specific gravity, and of a strongly acid reaction. The deposit is sometimes nearly white, but usually it is of a light pink or even red color, according to the degree of concentra-

tion of the urine from which it is deposited. If the urine be allowed to settle in a white earthen or porcelain vessel, and then carefully poured off, the more deeply colored deposits are left as a brick-red stain upon the inner surface of the vessel, forming what is known as the "brick-dust" sediment.

Deposits of the urates are easily recognized by two special characters, namely: First, they never appear while the urine is still warm, but only after it has cooled; the urine, when first passed, being always perfectly clear, and becoming turbid on repose, more or less rapidly according to the rate of cooling. Secondly, the urine, after cooling, however turbid, if heated in a test-tube, becomes clear again, usually before reaching the boiling point. Both these characters depend upon the solubility of the urates at high temperatures.

In rare cases, when a specimen of urine is turbid with the urates and also contains albumen, a double effect may be produced by the application of heat. When such a specimen is first heated, it is cleared up, owing to the solution of the urates; but, on approaching the boiling point, it again becomes turbid from precipitation of the albumen.

The urates are also soluble in the caustic alkalies, so that the addition of a few drops of a solution of sodium or potassium hydrate redissolves the precipitate. The addition of a free acid decomposes it, with the formation of a soluble salt, and the separation of uric acid which afterward crystallizes, as when thrown down in the same manner from normal urine. But the volume of the uric acid thus produced is so much smaller than that of the urates previously disseminated through the urine, that the immediate apparent effect is that of simple solution of the precipitate. A deposit of the urates is accordingly the only one liable to occur in the urine, which is cleared up by the addition of both alkalies and acids.

Deposits of the urates, when first thrown down, are pulverulent in form, presenting under the microscope only the appearance of a collection of minute granules. After a day or two they sometimes crystallize in the form of bundles or globular masses of radiating needles, often with straight or curved projections, extending from the outer surface. If a few drops of free acid be added to this deposit while under the microscope, the crystalline masses of sodium urate may be seen to grow transparent, and slowly dissolve

Fig. 131.

Crystalline Masses of Sodium Urate, from a urinary deposit.

from without inward, while rhomboidal tabular crystals of uric acid make their appearance in the adjacent fluid.

Crystals of uric acid sometimes appear spontaneously in a deposit of the urates within a few hours after its formation, owing to the development of a free acid in the urine; and they are sometimes formed within the urinary passages, so as to be present when the urine is first passed. Owing to their density and angularity they are the cause of much irritation to the mucous membrane of the bladder and urethra, and are known as the "gravel" of the urine. In a mingled precipitate of the urates and uric acid, the urates form an abundant light, pulverulent, pinkish turbidity; while the uric acid is a comparatively scanty, dense, deeply colored, crystalline deposit, which sinks rapidly and accumulates at the bottom of the vessel, the urates being more slowly deposited above it.

Blood.—Urine containing blood is more or less tinged throughout its mass with a dull reddish color which is easily distinguished from that due to a concentration of the normal color of the urine itself. After one or two hours of repose in a cylindrical glass vessel, the blood-globules are slowly deposited; and when, as frequently happens, they are entangled in minute filamentous coagula, these form a strongly colored red layer at the bottom of the vessel. The nature of the deposit is recognized by two well-marked characters, namely: 1st. The blood-globules are easily distinguished by microscopic examination, their natural form not being entirely lost even after they have remained in the urine for several hours; and 2d. The supernatant fluid, when decanted from the deposit, is found to contain albumen.

Mucus.—The slight quantity of vesical mucus which is normally contained in the urine is at first uniformly disseminated throughout its mass, and even after being left in repose is insufficient to produce any well marked or consistent deposit. The light cloudy opalescence, which it forms at the bottom of the vessel, is visible only on close inspection, and is readily disseminated again by the least agitation. But in cases of inflammation of the urinary bladder, the mucus discharged is much increased in quantity and altered in quality. It then appears as a consistent mass, which does not mix uniformly with the rest of the urine, but subsides to the bottom as a semifluid deposit. Mucus by itself is transparent and colorless, but it frequently contains a certain number of epithelium cells exfoliated from the inner surface of the bladder; and when crystalline or pulverulent deposits begin to take place in the urine, they occur first in contact with the mucus, so that its surface is often sprinkled with a thin layer of the urates or phosphates, which give it a partly opaque appearance. It is distinguished by its viscid and semifluid consistency. It is not affected by heat, but is coagulated and shrivelled by the action of alcohol and of nitric or acetic acid. Urine containing mucus is especially liable to rapid decomposition, and often has, soon after being discharged, a peculiarly offensive odor from this cause.

Pus.—When pus is contained in the urine it subsides on standing, and forms at the bottom a dense, homogeneous-looking, creamy-white layer. It is perfectly fluid in consistency and may be easily disseminated by agitation. Microscopic examination shows it to be composed exclusively of colorless, granular, nucleated "pus-globules," identical in appearance with the white globules of the blood, but distinguishable from those belonging to a deposit of blood by their much greater abundance and by the absence of red globules. If the supernatant fluid be poured off, and a few drops of a solution of caustic alkali added to the purulent deposit, it loses its white color and opacity, owing to the solution of its granular cells, and swells up into a transparent, colorless substance of gelatinous consistency, which can no longer be poured out of the vessel in drops, but slides out in a single semi-solid mass. This character alone will serve to distinguish a deposit of pus from any other liable to occur in the urine. The supernatant fluid, when carefully filtered, is found to contain a small quantity of albumen, the interstitial fluid of pus being itself albuminous.

Decomposition of the Urine.

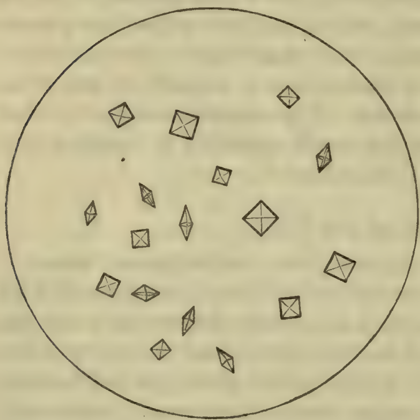
After its discharge from the body, the urine undergoes spontaneous changes, by which its ingredients are altered and finally disappear. This process of spontaneous decomposition is closely dependent upon the small quantity of mucus contained in the urine, since it is very much retarded if the mucus be separated by immediate filtration, and is hastened in a corresponding degree when the mucus is abnormally abundant. It is characterized by two different stages, which are distinguished from each other by the successive development of an acid and an alkaline reaction. They are known accordingly as the acid and the alkaline fermentations.

Acid Fermentation of the Urine.—This process, which is the first to show itself in the urine, takes place for the most part within the first twelve, twenty-four, or forty-eight hours after the discharge of the urine, according to the elevation of the surrounding temperature. It consists in the production of a free acid, usually lactic acid, from some of the undetermined organic ingredients of the excretion. The urine when fresh contains no free acid substance, its reaction to test-paper being due to the presence of its sodium biphosphate. But lactic acid has, notwithstanding, been so often found in nearly fresh urine as to be sometimes regarded as one of its normal constituents. Observation has shown, however, that urine, although entirely free from lactic acid when first passed, may present distinct traces of this substance after some hours of exposure to the air. Its production in this way, although not constant, appears to be sufficiently frequent to be regarded as a normal process.

During the period of the acid fermentation, there is reason to believe that oxalic acid is also sometimes produced in a similar manner. It is

certain that a deposit of lime oxalate is frequently present in perfectly normal urine after a day or two of exposure to the atmosphere, and may be observed, under these circumstances, without the existence of any morbid symptom. Whenever oxalic acid is formed in the urine it must unite with the lime in preference to any other of the bases present, and is consequently deposited under the form of lime oxalate; a salt which is quite insoluble both in water and in the urine, even when heated to the boiling point. In these cases, the lime oxalate crystals gradually appear in the light cloud of mucus collected at the bottom of the vessel, while the supernatant fluid remains clear. They are of minute size, for the most part just visible to the naked eye, rather scanty in amount, transparent, and colorless. They have the form of regular octohedra, or double quadrangular pyramids, united base to base. They make their appearance usually about the commencement of the second day, the urine at the same time continuing clear and retaining its acid reaction. They frequently appear as a deposit when no substance containing oxalic acid or oxalates has been taken with the food. The precise source from which the oxalic acid, under these circumstances, is derived has not been fully determined, but it is most probably produced from a metamorphosis of a small portion of the uric acid of the urine. If uric acid be boiled in two parts of water with lead peroxide, it is decomposed, with the production, among other substances, of urea and oxalic acid; and it is supposed that some similar change may take place in the urine, causing the appearance of a minute quantity of oxalic acid, which decomposes a portion of the lime salts and thus appears as a crystalline deposit of lime oxalate.

Fig. 132.



CRYSTALS OF LIME OXALATE, deposited from healthy urine, during the acid fermentation.

Alkaline Fermentation of the Urine.—At the end of a few days the changes above described come to an end, and are succeeded by a different process, which consists essentially in the decomposition of the urea of the urine and its transformation into ammonium carbonate. This change, which may be produced artificially in a watery solution of urea by continued boiling, takes place in the urine slowly at low temperatures, more rapidly during warm weather. The elements of two molecules of water unite with those of the urea undergoing decomposition, to produce ammonium carbonate, as follows:

$$\underset{\text{Urea.}}{CH_4N_2O} + H_4O_2 = \underset{\text{Ammonium carbonate.}}{(NH_4)_2CO_3}.$$

The first portions of the ammoniacal salt thus produced neutralize a corresponding quantity of the sodium biphosphate, so that the acid reaction of the urine diminishes in intensity. This reaction gradually becomes weaker, as the fermentation proceeds, until it at last disappears altogether and the urine becomes neutral. The production of ammonium carbonate still continuing, the reaction of the fluid then becomes alkaline, and its alkalescence grows more pronounced with the constant accumulation of the ammoniacal salt.

The time at which the alkaline reaction of the urine becomes established varies with its original degree of acidity and with the rapidity of its decomposition. Urine which is neutral when first passed, as often happens with that discharged during the earlier part of the day, will of course become alkaline more readily than that which has at first a strongly acid reaction. In the summer, urine will become alkaline, if freely exposed, on the third, fourth, or fifth day; while in the winter, a specimen kept in a cool place may still be neutral at the end of fifteen days. In cases of paralysis of the bladder accompanied with cystitis, where the vesical mucus is increased in quantity and altered in quality, and the urine is retained in the bladder for ten or twelve hours at the temperature of the body, it may change so rapidly as to be distinctly alkaline and ammoniacal at the time of its discharge. In these cases it is acid when first secreted by the kidneys, and becomes alkaline while retained in the interior of the bladder.

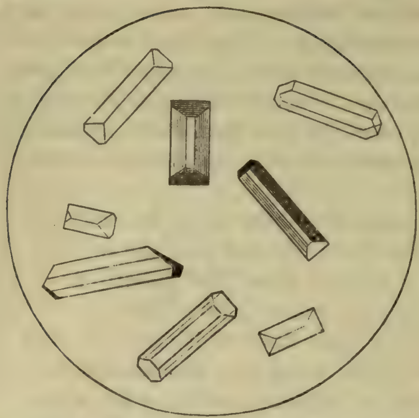
The first effect of the alkaline condition of the urine, thus produced, is the precipitation of the earthy phosphates. This precipitate slowly settles upon the sides and bottom of the vessel, or is partly entangled with certain animal matters which rise to the surface and form a thin, opaline scum upon the urine. There are no crystals to be seen at this time, but the deposit is entirely amorphous and granular.

The next change consists in the production of a new salt, the *ammonio-magnesian phosphate*, by the combination of the ammonia formed from the urea with the magnesium phosphate already present in the urine. The change may be represented as follows:

$$\underset{\text{Magnesium phosphate.}}{MgHPO_4} \quad + \quad \underset{\text{Ammonia.}}{NH_3} \quad = \quad \underset{\text{Ammonio-magnesian phosphate.}}{MgNH_4PO_4}$$

The crystals of this salt are very elegant and characteristic. They show themselves throughout all parts of the mixture, growing gradually in the mucus at the bottom, adhering to the sides of the glass, and scattered abundantly over the film which collects upon the surface. By their refractive power they give to this film a peculiar glistening and iridescent appearance, which is nearly always visible at the end of six or seven days. The crystals are perfectly colorless and transparent, and have the form of triangular prisms, generally with bevelled extremities. Their edges and angles are frequently replaced by secondary facets. They are insoluble in alkalies, but are easily dissolved by acids, even in very dilute form. At first they are of minute size, but gradually

Fig. 133.



CRYSTALS OF AMMONIO-MAGNESIAN PHOSPHATE, deposited from healthy urine, during the alkaline fermentation.

increase, so that after seven or eight days they may become visible to the naked eye.

As the decomposition of the urine continues, the ammonium carbonate which is produced, after saturating all the other ingredients with which it is capable of entering into combination, begins to be given off in a free form. The urine then acquires an ammoniacal odor; and a piece of moistened test-paper, held a little above the surface, will have its color turned by the alkaline gas escaping from the fluid. This is the source of the ammoniacal vapor given off wherever urine is allowed to remain and decompose. It continues until all the urea has been decomposed.

Renovation of the Body in the Nutritive Process.

As the materials of nutrition are constantly introduced with the food, while, on the other hand, the products of excretion are removed from the body and discharged externally by the breath, the perspiration, the urine, and the feces, an incessant renewal takes place in the ingredients of which the animal system is composed. During the early periods of growth and development, the quantity of material introduced is greater than that discharged, and the body consequently increases in weight and size. In wasting diseases and in advanced age, the loss of substance by excretion exceeds the gain by nutrition, and the weight of the body is therefore diminished. But during health, in adult life, the two processes are equal; and, with certain temporary fluctuations which counterbalance each other, the weight of the body remains the same.

The total quantity of material, introduced and discharged within a given time, forms, accordingly, a measure of the rapidity with which the internal changes of nutrition and metamorphosis go on in the animal system. It is not possible to indicate this quantity in either case with absolute accuracy; but the observations which have been made in this direction are sufficiently definite to show, in a general way, the average results of the two corresponding actions of waste and supply. The following table gives, approximately, the daily quantity of material absorbed and discharged in a healthy adult, the weight of the body remaining sensibly unaltered:

Absorbed during 24 hours.			Discharged during 24 hours.		
Water . . .	2250	grammes.	Carbonic acid . .	750	grammes.
Oxygen . . .	700	"	Aqueous vapor . .	500	"
Albuminous matter .	130	"	Perspiration . .	850	"
Starch and sugar .	300	"	Water of the urine .	1200	"
Fat	100	"	Urea and salts . .	70	"
Salts . . .	20	"	Feces . . .	130	"
	3500	grammes.		3500	grammes.

Rather more than 5 per cent., therefore, of the entire bodily weight is absorbed and discharged daily by the healthy adult human subject; and, for a man having the average weight of 65 kilogrammes, a quantity of material, equal to the weight of the whole body, thus passes through the system in the course of twenty days.

SECTION II.

THE NERVOUS SYSTEM.

CHAPTER I.

GENERAL STRUCTURE AND FUNCTIONS OF THE NERVOUS SYSTEM.

THE nervous system is an apparatus of intercommunicating fibres and cells, disseminated throughout the body, and standing in anatomical connection with the various organs of the animal system. It has properties which are different from those of the other organized tissues, and the effect of its operation is to bring the active phenomena of various parts of the body into a definite relation with each other, and with those of the outside world. It is therefore a medium of communication, by which the different animal functions are associated together in harmonious action, and are stimulated or modified according to the demands of the system itself or the varying influence of external conditions.

Each organ and tissue of the body possesses, independently of the nervous system, certain characteristic properties or modes of activity, which may be called into operation by any appropriate stimulus or exciting cause. If the heart of a frog, after its removal from the body, be touched with the point of a steel needle, it contracts and repeats very nearly the movement of an ordinary pulsation. If the leg of the same animal be separated from the thigh, the integument removed, and the poles of a galvanic battery applied to its exposed surface, a muscular contraction takes place at the moment the electric circuit is completed. The application of heat, friction, or an irritating liquid to a particular part of the integument brings on a local redness which again subsides after the removal of the exciting cause; and a solution of belladonna dropped upon the cornea, when absorbed by the tissues and brought in contact with the iris, produces a change in the condition of its fibres and a dilatation of the pupil. In these instances, the organ which performs the vital act is excited by the direct application of a stimulus to its own tissues.

But this is not the mode in which the natural functions of the animal system are excited during life. The physiological stimulus which calls

into action the organs of the living body is not direct but indirect in its operation. In the healthy and uninjured condition of the frame, the muscles are never made to contract by an external stimulus applied immediately to their own fibres, but by one which first operates upon some other organ, adjacent or remote. The various secreting glands have their functional activity increased or diminished by causes which are directly applied not to themselves but to other parts of the body; as where a flow of saliva from the parotid is produced by food introduced into the cavity of the mouth, or where the discharge of perspiration by the skin is modified by the influence of mental conditions. As a rule, therefore, in the natural state of the system, the various organs situated in different parts of the body are connected with each other by a mutual sympathy which regulates their physiological action. This connection is established through the medium of the nervous system.

The function of the nervous system is therefore *to associate the different parts of the body in such a manner, that stimulus applied to one organ may excite the activity of another.*

The instances of this mode of action are as numerous as the different vital phenomena. The stimulus of light falling upon the retina produces contraction of the pupil. The introduction of food into the stomach causes the gall-bladder to empty itself into the duodenum. The contact of alimentary substances with the mucous membrane of the intestine, excites the peristaltic action of its muscular coat. The presence of a growing fœtus in the uterus is accompanied by an increased growth of the mammary glands. Every organ is subservient, in the manifestation of its functional activity, to influences from other parts, of a structure different from its own.

General Structure of the Nervous System.

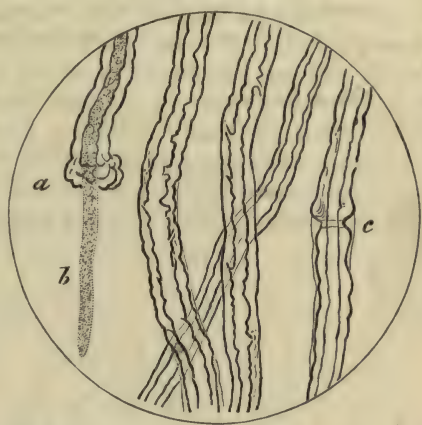
The nervous system consists of two kinds of nervous tissue, differing from each other in appearance, structure, and physiological endowments. One of these is the *white substance*, composed of nerve fibres alone; the other is the *gray substance*, which contains, in addition to the nerve fibres, interstitial matter and nerve cells. The white substance is found in the trunks and branches of the nerves, on the surface of the spinal cord, and in the internal parts of the brain. The gray substance forms the external layer or convolutions of the brain, as well as various deposits about its base and central parts, the central portion of the spinal cord, and a large number of small detached masses in different parts of the body. These two kinds of nervous tissue are so different in their properties and function as to require for each a separate description.

Nerve Fibres.

The nerve fibres are cylindrical filaments, arranged in bundles or tracts, in which they run, for the most part, in a direction parallel to each other. Their diameter varies considerably, even in the same

locality; some of the fibres in a single bundle being 10, 15 or 18 micromillimetres in diameter, while others are not more than 2.5 mmm. Their average size also varies in different parts of the nervous system. The larger fibres are found in the peripheral trunks and branches of the nerves, where they have an average diameter of 12.5 mmm.; in the white substance of the brain and spinal cord their average diameter is 5 mmm., and in the gray substance it is reduced to 2 mmm. Two portions of the nervous system, both of which contain nerve fibres, are often distinguished from each other by the relative numbers of their larger and smaller fibres. Thus in the cutaneous nerves of man, according to Bidder, Volkmann, and Kölliker, the larger and smaller fibres are present in about equal quantity, while in the muscular nerves the larger fibres are three times as abundant as the smaller. In the nerves of bony tissue the proportion of small fibres is double that of the large ones, and in the gray substance of the cerebral hemispheres there are none larger than 6 or 7 mmm. in diameter. The nerve fibres belonging to the same bundle or tract may even become increased or diminished in diameter in different parts of their course; as Kölliker has shown that the fibres of the posterior roots of the spinal nerves, in passing through the cord from the exterior to the gray substance, are reduced in their average diameter from 10 to 5 mmm.; and those of the white substance, of the cerebral hemispheres, on entering the gray matter of the convolutions, are reduced from 5 mmm. to 2 mmm. in diameter.

Fig. 134.



NERVE FIBRES from the Sciatic Nerve.—At *a*, the torn extremity of a nerve fibre with the axis cylinder (*b*) protruding from it. At *c*, the medullary layer is nearly separated by accidental compression, but the axis cylinder passes across the injured portion. The outline of the tubular membrane is also seen at *c* on the outside of the remaining portions of the fibre.

The structure of the nerve-fibre, in its most complete form, presents three distinct elements, namely: an external tubular sheath, an intermediate medullary layer, and a central axis cylinder.

The Tubular Sheath.—The exterior of the nerve fibre is composed of a colorless, transparent tubular membrane, which closely invests the remaining portions and is seen with some difficulty in the natural condition of the fibre, owing to its extreme thinness and delicacy. It may often, however, be distinguished at certain points where the nervous fibre is accidentally compressed or indented, as at *c*, Fig. 134; or it may be brought into view for considerable distances according to the method of Kölliker, by treating the fibres with a cold

solution of sodium hydrate, and afterward boiling them for an instant in the same fluid. This extracts the greater part of their contents, and leaves the tubular sheath in the form of an empty cylindrical canal. In its general chemical relations, the tubular sheath is similar to the sarcolemma of muscular fibre, its principal physical properties being its cohesion and elasticity. Its physiological function is undoubtedly that of a protecting envelope, by which the internal portions are maintained in place and preserved from mechanical injury.

The Medullary Layer.—Immediately within the tubular sheath is a layer of transparent, highly refractive, nearly fluid material, of oleaginous consistency, termed the medullary layer, or medulla, which gives to the nerve fibres, and the tracts composed of them, a white and shining aspect. This substance is readily altered by a diminution of temperature, or by the contact of unnatural fluids, even by exposure to the air or the imbibition of water, or by the ordinary manipulations required in preparing it for microscopic examination. Under these influences it undergoes a sort of coagulation, being increased in density and in refractive power, so that both its external and internal limits are indicated by a dark and strongly marked outline. This gives to the nerve fibre the very characteristic appearance of a cylinder with a double contour, presenting two distinct parallel outlines at each edge; an appearance by which it may be easily distinguished from any other anatomical element. As the coagulation of the medullary layer goes on, its outlines become more or less irregular, and after a certain time it involves the whole of the fibre in a more or less confused mass of irregularly refracting substance. The fibres containing a medullary layer, and exhibiting the characteristic double contour due to its presence, are called "medullated nerve fibres."

In the smaller variety of nerve fibres from the substance of the brain and spinal cord, the external tubular sheath is wanting, or at least cannot be demonstrated; and such fibres, owing to their want of support and their soft consistency, are readily distorted by accidental pressure, or by the contact of reagents. They become swollen or varicose at many points; and the medullary substance is forced out or exudes from their torn extremities in irregularly globular, fusiform, or filamentous masses, which show on their exterior the double contour due to a superficial coagulation. These detached

Fig. 135.

NERVE FIBRES, from the white substance of the brain.—*a, a, a* Portions of the myeline, pressed out, and floating in irregularly rounded drops.

portions, which are everywhere visible in ordinary microscopic preparations of the brain substance, are termed "myeline drops," and owe their peculiar appearance to the nature of the ingredients which form the medullary layer of the nerve fibre. The medullary layer is composed of a substance termed *myeline*, which is not, however, a distinct proximate principle, but is itself a mixture of various different materials. It consists mainly of cerebrine, a nitrogenous matter found only in the nervous centres, together with a large proportion of cholesterine and fat. There is also a certain proportion of lecithine, a nitrogenous and phosphorized matter, which is also found in the gray substance. The mixture of these ingredients gives to the myeline its peculiar consistency and reaction.

In regard to its physiological function, the medullary layer of the nerve fibre is generally considered as an isolating substance, like the gutta-percha envelope of a submarine telegraph wire, so arranged as to confine the transmission of nerve force within proper limits, and prevent its diffusion to neighboring parts. We have no absolute proof that such is its true character, but there are some facts which lend a certain probability to this view. The medullary layer exists throughout the main portion of a large majority of the nerve fibres, where they transport the nervous stimulus uninterruptedly from one point to another; but they are destitute of it both at their origins and terminations, where they come in contact with the elements of the gray matter, or are connected with the peripheral organs of sensation and motion. Whatever may be its exact function, therefore, the medulla evidently plays a secondary, and not a principal part, in the physiological action of the nerve fibre.

The Axis Cylinder.—The central part of the nerve fibre consists of a pale, homogeneous, or finely granular cord, of a cylindrical or slightly flattened form, occupying the position of the longitudinal axis of the fibre. From these characters it has received the name of the "axis cylinder." It differs from the medullary layer, by which it is enveloped, in consistency; for while the latter is nearly fluid in its natural condition, the axis cylinder is solid, and, though very delicate, possesses a certain degree of elasticity. By some observers (Schultze, Gerlach) the axis cylinder is regarded as composed of many excessively minute fibrillæ, united into a uniform bundle; by others of equal authority (Kölliker) the indications of such a fibrillated constitution of this part of the nerve fibre are considered as uncertain.

The axis cylinder is composed of an albuminous substance which is insoluble in water, alcohol, and ether; becomes pale and swollen by the action of concentrated acetic acid; and is readily dissolved by a boiling solution of sodium hydrate. It is stained red by treatment with a solution of carmine, while the enveloping medullary layer remains uncolored; and by this means a visible distinction may be made between the two. The application of a solution of gold chloride, and subsequent exposure to light, stains the axis cylinder of a dark purple, nearly

black color; and by this mode of preparation nervous fibres of extreme delicacy have been traced among surrounding tissues, where they would otherwise escape observation.

In its physiological properties, the axis cylinder is undoubtedly the most essential element of the nerve fibre, since it is the only one universally present, and always extending throughout the whole length of a fibre from its origin to its termination. Its albuminous nature also distinguishes it from other parts of the nerve fibre, and indicates the relative importance of its function. It is probably through the axis cylinder that the passage of the nerve current takes place, and in its substance that the principal changes accompanying this action are effected.

Non-Medullated Nerve Fibres.—Beside the nerve fibres constituted, as above, by an axis cylinder, surrounded by a medullary layer, with or without an external tubular membrane, there are others which consist of the axis cylinder destitute of any medullary layer, and which consequently do not exhibit the appearance of a double contour. These are called "non-medullated nerve fibres." They are found, in man, only in certain parts of the sympathetic nerves, in the terminal nervous expansions of the muscles and organs of sense, and in the nervous centres in the immediate vicinity of the cells of the gray substance. In the sympathetic nerves, they are, for the most part, mingled with a considerable proportion of medullated fibres, though some of the sympathetic branches distributed to the intestine and the spleen, according to Schultze, are composed of non-medullated fibres exclusively. The branches of the olfactory nerve, distributed to the nasal mucous membrane, also consist altogether of fibres of this kind. Such nervous branches have not the white, opaque aspect belonging to other nerves, but are grayish-looking and semi-transparent in appearance; a peculiarity which is evidently due to the absence of the myeline or medullary layer.

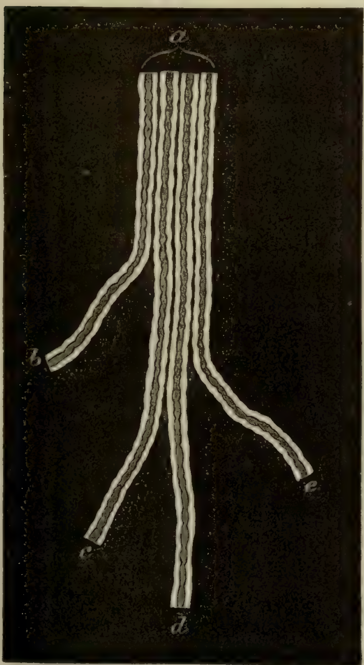
The same nerve fibre may be medullated for the greater part of its course, and become destitute of medulla at its termination, as is the rule with the cerebro-spinal nerves generally; or fibres may originate in the gray substance as non-medullated axis cylinders, and become invested, after a short distance, with a distinct medullary layer. The non-medullated nerve fibres are not, therefore, regarded as essentially different from the others, but only as presenting a less complicated form of structure.

Course and Mutual Relation of the Nerve Fibres.—In the white substance of the brain and spinal cord, the nerve-fibres form continuous tracts, of larger or smaller size, lying in contact with each other, and not mingled with any considerable proportion of other tissue. But on passing out of the bony cavities toward the exterior, they become collected into small bundles, each of which is invested with a thin prolongation of connective tissue, derived from the dura mater and periosteum; these bundles are associated into larger ones which are held together by a denser layer of the same connective tissue; and

finally the whole are united into a single compound mass by its exterior investment, which is known as the "neurilemma." Such a complete bundle is called a *nerve*, and the nerve fibres of which it is composed are usually all distributed, after a longer or shorter transit, to associated organs, or to adjacent regions of the body.

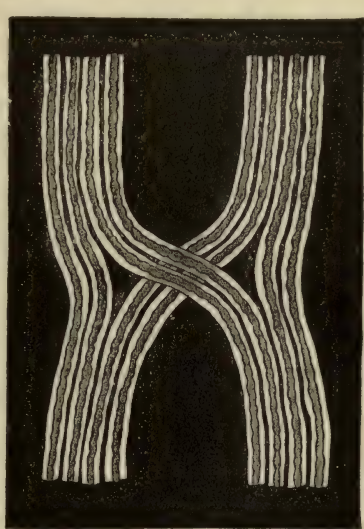
The nerve fibres themselves are not known to divide, branch, or inosculate with each other in any part of their course through the main trunks and branches of the nerves. So far as observation goes, each nerve fibre is continuous and independent, from its origin in the nervous centres to within a microscopic distance of its peripheral termination. When a nerve therefore divides during its course into several branches, or when the branches of adjacent nerves inosculate with each other to form a plexus, like the cervical, brachial, or lumbar plexuses, this is only because certain ultimate nerve fibres, or bundles of fibres, leave those with which they were previously associated, and pursue a different

Fig. 136.



DIVISION OF A NERVOUS BRANCH (*a*), into its ultimate fibres, *b*, *c*, *d*, *e*.

Fig. 137.



Inosculation of NERVES.

direction. A nerve which originates, for example, from the spinal cord and runs down the upper extremity, to be finally distributed to the integument and muscles of the hand, contains at its point of origin all the filaments into which it is afterward divided, and which are merely separated at successive points from the main bundle. In case of the inoscu-

lation of two nerves, the communication between them is effected by some of the fibres belonging to the first passing over from it to join the second, while some of those belonging to the second may also cross and join the first; the individual fibres in each instance remaining distinct, and retaining their identity throughout. In whatever way, therefore, the nerve fibres are associated in the various trunks and branches of the nerves, they may still act independently and preserve their specific functions in every part of their course.

Peripheral Termination of the Nerve Fibres.—Near the termination of the nerve fibres in the tissues to which they are distributed, they present certain important modifications both in structure and arrangement.

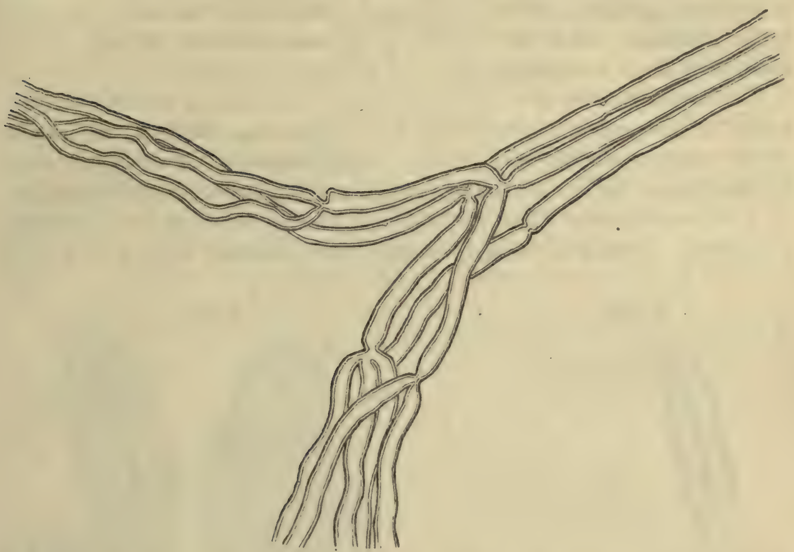
First, the smaller nervous branches, or bundles of nerve fibres, after penetrating the substance of the tissues, suddenly divide and subdivide with unusual rapidity; and these subdivisions, uniting with each other by inosculation, form abundant *plexuses*, from which are given off the individual fibres supplying the anatomical elements of the tissues. In the skin there are two such nervous plexuses, a deeper and a more superficial, of which the latter is the more closely set and composed of more slender bundles, containing only one or two fibres each. As a general rule, also, in other tissues, the last or terminal plexus is the finest, and incloses between its meshes the narrowest interspaces. The nerve fibres, on reaching the situation of the terminal plexus, are also considerably reduced in size, being diminished both in the skin and the muscles from 10 or 15 mmm. to 4 or 5 mmm. in diameter. According to Kölliker it is sometimes possible to observe this diminution in the size of a single nerve fibre in different parts of its course through the muscular tissue.

Secondly, both in the terminal plexus and the branches given off from them, the *nerve fibres themselves undergo division;* so that a single fibre in this situation may give rise to two or more branches, each branch retaining all the original anatomical characters of a nerve fibre. There is usually a marked constriction at the point where the nerve fibre divides; but this is followed by a corresponding enlargement, so that the secondary fibres soon become nearly or quite equal in diameter to that from which they were derived. A nerve fibre may accordingly pass undivided, so far as we know, throughout its course in the roots, trunks, and principal branches and ramifications of the nerve, and may then, shortly before its termination, break up into a number of separate but closely adjacent secondary fibres. It has been estimated by Reichert, that, in the subcutaneous muscle of the frog, ten primitive nerve fibres may give rise by their division, to about 300 terminal extremities.

Thirdly, the nerve fibre, when near its peripheral termination, becomes altered in structure. This alteration consists in a disappearance of the medullary layer, by which the fibre loses its double contour; and by a similar disappearance or a separation of the tubular sheath. The nerve fibre, thus altered, is reduced, in its constituent parts, to the axis

cylinder alone; that is, all the secondary elements of its structure are lost, and there remains only the essential conducting filament of the

Fig. 138.



DIVISION OF NERVE FIBRES, in a small branch from the subcutaneous muscle of a frog. (Kölliker.)

axis cylinder. Lastly the nerve fibre, at the point of its final termination, is frequently brought into relation with cell-like bodies, which are sometimes regarded as analogous in character to the nerve cells of the gray substance in the nervous centres.

The ultimate termination of the nerve fibres in the skin has been most distinctly seen in the so-called "Pacinian bodies" and the "tactile corpuscles." The Pacinian bodies are ovoid-shaped masses from 1 to 4.5 millimetres in length, found in the subcutaneous connective tissue of the hands and feet, and various other parts of the body, consisting of a series of concentric laminæ of connective tissue, with a central cavity, inclosing a transparent, colorless, fluid or semifluid material. A single ultimate nerve fibre penetrates the Pacinian body at one extremity, and passes into its central cavity. At the point of entrance, the external tubular sheath leaves the nerve fibre and becomes continuous with the connective tissue laminæ of the Pacinian body. The medullary layer also disappears, and the nerve fibre, thus reduced to its axis cylinder, runs longitudinally through the greater part of the central cavity and terminates, toward its farther end, in either one or several slightly rounded extremities. The "tactile corpuscles," found in the sensitive papillæ of the skin of the hands and feet, are similar in form to the Pacinian bodies, but of much smaller size; having an average length,

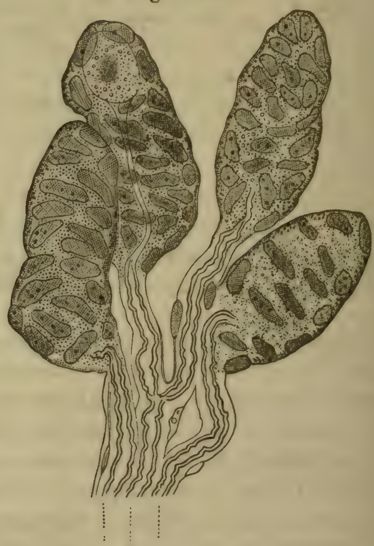
in man, of about 100 mmm. They consist each of a central, transparent, gelatinous mass, surrounded by an envelope of connective tissue, which is marked by many tranverse elongated nuclei. Each corpuscle receives one or two nerve fibres which run upward, in either a straight or spiral course, and, after losing their medullary layer, in some instances reach the central gelatinous nucleus, though for the most part their terminations are not distinctly visible.

The simplest form of tactile corpuscle is that known as the "terminal bulbs" of the sensitive nerves, in the conjunctiva, the lips, the papillæ of the tongue, and the soft palate. They are round or elongated ovoid bodies, consisting of a closed sac of connective tissue, sometimes marked with transverse nuclei, and containing a homogeneous or finely granular substance. Into this body is received the ultimate branch of a nerve

Fig. 139.

Terminal Bulb of a sensitive nerve; from the conjunctiva of the calf. (Frey.)

Fig. 140.



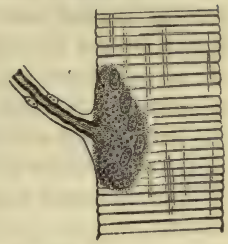
Tactile Corpuscles, from the edge of the tongue of the sparrow.—1, 2, 3. Medullated nerve fibres supplying four tactile corpuscles. One fibre divides into two branches; and one of them is traced to near the extremity of the corresponding corpuscle, where it ends in a cell-like expansion. (Ihlder.)

fibre, which is reduced to its axis cylinder and terminates in the interior by a free extremity. In some regions, as, for example, the lips in the human subject, and the tongue in birds, are to be seen structures which are intermediate in form between the terminal bulbs and the tactile corpuscles.

In the muscles, as a rule, each muscular fibre has, connected with it, at least one nerve fibre, and sometimes more than one. The ultimate

nerve fibre, given off as a branch from the terminal plexus, approaches the muscular fibre, usually at a right angle, and penetrates its exterior; the tubular sheath of the nerve fibre becoming continuous with the sarcolemma. At the same time its medullary layer ceases abruptly, and the axis cylinder spreads out into a thin oval expansion of granular matter interspersed with nuclei, called the "terminal plate," and lying in immediate contact with the contractile substance of the muscular fibre. Some variations in the form and disposition of the axis cylinder in the terminal plate are to be seen in the muscles of amphibia; but the above represents its essential characters in the muscles of birds and mammalians.

Fig. 141.



TERMINATION OF A NERVE FIBRE in muscular fibre, from the fowl. (Rouget.)

Physiological Properties of the Nerve Fibres.—The nerve fibres are organs of communication. They serve as connecting filaments between the nervous centres on the one hand and the peripheral organs of sensation and motion on the other. For this purpose they are endowed with a power of irritability by which, when excited at one or the other extremity, they transmit the nervous impulse throughout their entire length, and produce a corresponding effect at their opposite termination. Thus the nerve fibres distributed to the skin, when excited at their peripheral extremities, produce in the brain a sensation corresponding to the external impression. On the other hand, those which are distributed to the muscles, when excited at their origin by the impulse of the will, produce a contraction in the muscular fibres at their periphery. This physiological action produces no visible change in the nerve fibre itself. Its effects are manifest only at the extremities of the nerve, in the organs where it terminates. Nevertheless, it is evident that the nerve fibre serves to communicate in some way an action from one of its extremities to the other; since, if it be divided in any part of its course, the communication at once ceases, and sensation can no longer be perceived from impressions made upon the skin, nor voluntary contraction excited in the muscles.

Owing to the different effects thus produced, at their central and peripheral extremities, the nerve fibres and the nerves composed of them have been distinguished by different names. Those which transmit the stimulus of sensation, from the periphery to the nervous centres, are called *sensitive* nerves or nerve fibres; those which transmit the stimulus of motion, from the nervous centre outward to the muscles, are called *motor* nerves or nerve fibres. As a general rule, both sensitive and motor nerve fibres are associated together in the same nervous bundle, and separate from each other only when near their final distribution in the skin or mucous membranes on the one hand, and in the muscles on the other. But in some situations, near the origin of the nerves as well as near their termination, the sensitive and motor fibres run in distinct

bundles; as for example in the sensitive and motor roots of the fifth pair of cranial nerves, and in the anterior and posterior roots of the spinal nerves generally. The fibres belonging to the facial nerve are all motor fibres, making this exclusively a motor nerve. The three branches of the fifth pair, on the other hand, which are distributed to the integument and mucous membranes of the face, are composed exclusively of sensitive fibres; while the branch of the same nerve distributed to the muscles of mastication is made up principally or entirely of motor fibres.

No essential distinction has been discovered in the anatomical characters of sensitive and motor nerve fibres. In nerves and nervous branches which perform a motor function, the nerve fibres, as a rule, are of comparatively large size, averaging 15 mmm. in diameter; while in those performing a sensitive function they are smaller, averaging not more than 10 mmm. in diameter, and many of them being considerably less. But this difference is only one of proportion in numbers between the larger and smaller fibres; since both large and small fibres are found in both motor and sensitive nerves. Even in the motor nerves, the large fibres become reduced to the size of the smaller ones before their termination in the muscular tissue; and the nerve fibres generally are diminished or increased in diameter on passing into or out of the gray substance of the nervous centres. No absolute distinction therefore can be made between sensitive and motor nerve fibres as regards their size; and in regard to the essential details of their structure, namely, the tubular sheath, the medullary layer, and the cylinder axis, they are to all appearance completely identical.

Effect of Division upon the Nerve Fibres.—The immediate effect of dividing or seriously injuring the nerve fibres is a suspension of their physiological function. The physical communication being cut off between their extremities, the sensitive fibres can no longer transmit an impression from the skin to the nervous centre, and the motor fibres can no longer convey the stimulus of voluntary motion from the nervous centre to the muscles. In addition to this result, when the divided nerve fibre is permanently separated from its central connections, there also follows a change in its texture, which is propagated mainly in one direction, and which consists in an atrophy or degeneration of the nervous substance. The most distinct effects of this degeneration of a divided nerve fibre are to be seen in its medullary layer. According to the observations of Vulpian and Philippeaux, the alteration in structure, which takes place from the point of division toward the periphery, begins to be perceptible in mammalians, by microscopic examination, at the end of five days. The transparency of the fibre is first diminished, its contents having a more or less cloudy appearance. At the end of eight or ten days, the double contour of the fibre has become irregular and at various points partially or completely interrupted; and the substance of the medullary layer is broken up into separate masses of varying size, presenting the appearance of a coagulation and dislocation.

As the process goes on, the continuity of the medullary layer is entirely destroyed, and this substance is reduced to the condition of isolated oily-looking drops, scattered through the interior of the tubular sheath, which become gradually transformed into a diffused mixture of minute granules. Finally, the granules themselves disappear, and the tubular sheath, partially emptied by the atrophy of the medullary layer, becomes collapsed and wrinkled. The nerve which has suffered these changes has lost its white glistening color, and has assumed a grayish hue. The axis cylinder either does not participate in the above alterations, or its changes are not so manifest to the eye; since, according to some observers, it remains visible after the medullary layer has disappeared.

According to various observers (Waller, Krause, Vulpian), the degeneration of divided nerve fibres, both in the sensitive and motor nerves, may be propagated throughout their peripheral extremities, extending even to the sensitive papillæ of the tongue and the tactile corpuscles of the skin. Vulpian[1] has found that in dogs, six weeks after the division of the sciatic nerve, no nerve fibres could be discovered in the muscles of the foot which had not undergone the same alteration.

The rapidity with which degeneration takes place in the fibres of a divided nerve varies with the species and age of the animal to which it belongs. The change is less rapid in the cold-blooded, more so in the warm-blooded animals. In those of the same species, it goes on more quickly in the young, more slowly in animals which are fully grown. According to Vulpian, in young dogs, as a general rule, the disappearance of the medullary layer is complete at the end of six weeks or two months from the date of the injury.

The degeneration of the peripheral portions of divided nerves has often been utilized in order to determine the source of particular bundles of nerve fibres. If a nerve, for example, receives roots or communicating branches from two different sources, and afterward supplies by its ramifications several organs, it may be ascertained whether the fibres coming from one source are or are not distributed to a particular organ. For this purpose the root or communicating branch in question is divided; and when the subsequent process of degeneration is complete, the atrophied nerve fibres derived from this source may be followed by microscopic examination throughout their course, and recognized in the organ to which they are distributed.

Union and Regeneration of divided Nerves.—The loss of function in a divided nerve is not permanent; but, if the neighboring parts be healthy and no other injury have been inflicted, the nerve fibres may reunite, and their power of communication be restored. When the division has been a simple one, the two extremities of the divided nerve remaining in contact or in close proximity with each other, their union takes place with comparative readiness; but even when a considerable

[1] Leçons sur la Physiologie du Système Nerveux. Paris, 1866, p. 243.

portion of the nerve has been cut out, there may be a reproduction of the lost parts, and the nerve may finally regain its natural continuity. The fibres of new formation, thus produced, are at first of small diameter and of grayish aspect. They gradually increase in size, become provided with a medullary layer, and at last present all the anatomical characters of the healthy nerve fibre. Schiff, Vulpian, and Philippeaux have found that it is possible for the continuity of a nerve to be re-established, after the excision of portions of its trunk equal to five or even six centimetres in length. According to Vulpian, in very young animals, a loss of nerve substance from one to two centimetres in length may be restored at the end of six weeks; and the same observer has seen, in young rats, a portion of the sciatic nerve, six millimetres long, reproduced in the course of seventeen days.

At the same time, the degenerated portion of the nerve, situated beyond the point of its division, becomes restored. There is a reproduction of the medullary layer, which had become atrophied by the degenerative process, and the entire nerve again exhibits its normal anatomical character. The time required, for the complete regeneration of the peripheral portion of a divided nerve, is in general from three to twelve months, according to the age and species of the animal upon which the experiment is performed.

The complete regeneration of a divided or exsected nerve is indicated by the restoration of its normal function. If it be a sensitive nerve, the power of sensation, which was at first lost, returns in that portion of the integument to which its fibres are distributed; if it be a motor nerve, the power of voluntary motion is regained in the corresponding muscles. The observations of Vulpian have shown that, after the excision of the central extremity of the hypoglossal nerve in dogs, its peripheral portion may become capable of exciting contraction in the muscles of the tongue at the end of four months;[1] and according to those of Schiff upon young dogs and cats, sensibility may reappear in the tongue and lip in fourteen days after the excision of portions of the lingual and infra-orbital nerves, from two to two and a half centimetres in length.

In the human subject, at least in adult life, the restoration of divided nerves is much less rapid; and, according to L'Etiévant[2] and Weir Mitchell,[3] often either does not take place at all, when the injured nerves are of considerable size, or does so very imperfectly.

The smaller nervous branches supplying the skin are frequently divided by accidental incisions, causing a local anæsthesia, or loss of tactile sensibility in the immediate neighborhood. This anæsthesia persists usually for weeks, or even months, after the healing of the wound; but it almost invariably disappears at last, and the skin re-

[1] Leçons sur la Physiologie du Système Nerveux. Paris, 1866, p. 272.

[2] Traité des Sections Nerveuses. Paris, 1873.

[3] Injuries of Nerves, and their Consequences. Philadelphia, 1874, p. 84.

covers its normal sensibility. Restoration may also undoubtedly take place in nerves of larger size, as in the case reported by L'Etiévant,[1] where the median nerve was divided in a man twenty-six years of age, at the upper third of the arm. The power of motion and sensibility, dependent on the fibres of this nerve, remained abolished for ten months, but began to reappear in fourteen months, and were almost completely restored at the end of a year and a half.

Nerve Cells.

The nerve cells, which form the characteristic anatomical element of the gray substance, are rounded or irregularly shaped bodies, consisting of a soft, semi-transparent, finely granular, albuminous matter, and containing a rather large, distinctly marked nucleus and nucleolus. Sometimes they also contain a certain quantity of brown, yellowish, or blackish pigment grains, which are especially abundant in the immediate neighborhood of the nucleus. The nerve cells vary in size in different parts of the gray substance. The smaller ones, from 10 to 20 mmm. in diameter, are found in the ganglia of the sympathetic system, the convolutions of the cerebral hemispheres, and in the posterior horns of gray matter in the spinal cord. The larger, averaging from 40 to 60 mmm., are in the convolutions of the cerebellum, and in the medulla oblongata; the largest of all, as a general rule, being met with in the anterior horns of gray matter of the spinal cord, where they reach the diameter of 130 or 135 mmm., or seventeen times the size of the red globules of the blood.

Fig. 142.

NERVE CELLS from the gray substance of the medulla oblongata. (Dean.)

The most marked anatomical features of the nerve cells are their *prolongations*. These are narrow processes or extensions of the cell substance, and consisting apparently of the same material. In the ganglia of the sympathetic system, and in those situated upon the roots of the spinal and cranial nerves in man, the nerve cells have for the most part a rounded form, and only one or two prolongations. Throughout the gray substance of the brain

[1] Traité des Sections Nerveuses, p. 54.

and spinal cord, on the contrary, they present three, four, five, or even eight prolongations, running in different directions and giving to the cell a peculiar radiated appearance. The prolongations after a certain distance become branched, the branches thus formed again dividing and subdividing, growing at the same time smaller in size, until they terminate in a more or less abundant tuft or ramification of exceedingly slender filaments. According to Gerlach, the terminal fibres of this ramification constitute a plexus of fine nervous threads, penetrating the interstitial substance of the gray matter. It is not, however, known with certainty whether these fibres terminate by free extremities, or whether they form a network of communication between different nerve cells.

Connection between the Nerve Cells and Nerve Fibres.—In all cases the nerve fibres are connected, at their central origin, with masses of gray substance, into which they penetrate and in which they are intimately mingled with the nerve cells. In some instances, a direct continuity can be seen between the nerve fibres and certain prolongations of the nerve cells; in others, such a direct anatomical connection is only rendered more or less probable by the similarity in direction between the nerve fibres and the processes of the nerve cells, and by their resemblance in physical constitution.

In the ganglia of the sympathetic system and in those of the roots of the spinal and cranial nerves, the nerve cells of a rounded form give off, as a rule, in man and the mammalians, only a single, pale, undivided process, which at first presents the appearance of an axis cylinder of small diameter, but which subsequently increases in size and becomes provided with a medullary layer, assuming at the same time the distinct double contour, characteristic of a fully formed nerve fibre. These cells, sending out a single nerve process in one direction, are called "unipolar" nerve cells. In the ganglia of the spinal nerve roots, and in the Gasserian ganglion of fishes, nerve cells are found which send off two such processes in opposite directions; the medullary layer of the nerve fibre ceasing on each side just before its union with the body of the cell. Such cells, with two opposite nerve processes, are called "bipolar" nerve cells. These connections have been recognized by all observers, and there is no doubt as to their existence.

In the gray substance of the brain and spinal cord, the nerve cells, as above described, are "multipolar," or send out a number of prolongations, in different directions, which divide and ramify without making any certain anatomical connection with other parts. Beside these branching prolongations, however, according to the observations of Deiters, confirmed by Schultze, Gerlach, and Kölliker, the multipolar nerve cell also sends out a single prolongation which is different from the others, in that it does not branch but continues on its course for a considerable distance, presenting the usual physical aspect of a naked axis cylinder. This simple unbranched process is called the "axis cylinder process," to distinguish it from the remaining ramified pro-

longations. Cells of this description, provided both with ramified prolongations and with a single unbranched axis cylinder process, are found abundantly in the spinal cord, the medulla oblongata, the cerebellum, the corpora striata, and the optic thalami. The axis cylinder process, in the spinal cord, passes into the bundles of medullated nerve fibres forming the roots of the nerves and the columns of the cord; and in the convolutions of the cerebellum and the cerebral ganglia, the nerve fibres which penetrate the gray substance lose their medullary layer and become reduced to the condition of a naked axis cylinder, similar in appearance to the prolongations of the nerve cells. For these reasons it is considered probable that the nerve fibres are connected by continuity of substance with the axis cylinder process of the nerve cells. But, according to the most careful observers,[1] this connection is more or less hypothetical, and is not positively shown by direct observation. It is evident that there is a physiological communication between the nerve fibres and the nerve cells; but it is possible that such a communication may take place by other methods than an immediate continuity of their substance.

Finally, it is certain that there are nerve cells in the gray matter which are not directly connected with nerve fibres. According to the observations of Gerlach, there is a tract throughout the dorsal portion of the spinal cord, near the central part of its gray substance, where all the nerve cells are provided with branching prolongations, but do not possess any undivided process resembling a cylinder axis. It is not known whether such cells exist also in other portions of the nervous system.

Physiological Properties of the Nerve Cells.—The nerve cells, and the gray substance of which they form a part, act as centres, in which the nervous impressions are received through the sensitive nerve fibres from the periphery, and from which a stimulus is sent out through the motor fibres to the muscles. Every collection of gray substance is therefore called a "nervous centre." While the nerve fibres accordingly are organs of transmission only, the gray substance and its nerve cells constitute an apparatus in which the nervous influence is modified in character, and changed from one form to another. Their function is to receive impressions conveyed to them by the nerve fibres, and to convert these impressions into impulses which are transmitted to distant organs. The nature of the process by which this change is effected, and the action which goes on in the nerve cells during its accomplishment, are entirely unknown to us; but it is evidently essential to the physiological operation of the nervous system, since neither sensation nor movement is ever excited, in the natural condition, through the nerve fibres, unless they are in communication with the gray substance of a nervous centre.

[1] Kölliker, Eléments d'Histologie Humaine, 5me édition. Paris, 1868, pp. 361, 363, 365, 399.

Reflex Action of the Nervous System.—The nervous system thus stands as a medium of communication between different parts of the living body, so that a stimulus applied to one organ may excite the activity of another. This communication between adjacent or distant parts is never direct, but always a circuitous one. It passes invariably through an intermediate nervous centre, which receives the impression conveyed to it by nerve fibres from one organ, and reacts by sending out a stimulus which calls into activity the other. This is called the "reflex action" of the nervous system, because the stimulus is first sent inward to the nervous centre and then returned or reflected in the opposite direction. In this process, the intermediate act between the inward and outward passage of the nervous stimulus is accomplished in the gray substance of the nervous centres.

CHAPTER II.

NERVOUS IRRITABILITY AND ITS MODE OF ACTION.

The property possessed by nerves of being called into excitement by an appropriate stimulus is termed their "irritability." This property is not confined to the elements of the nervous system, but exists also in other tissues and organs. Each organ or anatomical element, when subjected to the application of a stimulus adapted to its physiological character, reacts in a way peculiar to itself and produces a visible result of a definite kind. Thus a glandular organ, when excited, exhibits the phenomena of secretion; a muscle or a muscular fibre, those of contraction. The visible result of glandular activity is the accumulation and discharge of the secreted fluids, that of muscular contraction is a change of form in the muscle, and a movement of the parts to which it is attached. The irritability of a nerve or a nerve fibre, on the other hand, is not manifested by any perceptible change in its own substance, but by the phenomena of sensation or motion in the organs to which it is distributed.

Irritability of Sensitive Fibres.

The irritability of the sensitive nerve fibres is most directly manifested during life by the production of sensation. This sensation, however, does not exist in the nerve itself, but in the nervous centre where its fibres terminate. The proof of this is that if the communication between any part of a sensitive nerve and the brain be cut off by division of the nerve fibres, no stimulus subsequently applied to the separated trunk or branches of the nerve will produce any perceptible sensation. If, however, the connection between the nerve and the nervous centre be retained, while that with the external integument be cut off, stimulants of various kinds applied to the nerve itself will produce a sensation which is more or less acute according to the stimulus employed. Pinching or pricking the nerve, variations of temperature, or the passage of an electric current, will all have the effect of bringing into action the nervous irritability, and thus producing the effect of a sensation.

In order to accomplish this result, however, two conditions are essential. First, the nerve must be, as above mentioned, in communication with the nervous centre where the sensation is to be perceived; and secondly, the nerve fibres themselves must retain their power of irritability. The irritability of a sensitive nerve may be so deadened

by the compression of a bandage or the application of cold, that no stimulus applied to the part will produced any perceptible effect. According to the observations of Weir Mitchell,[1] the application of extreme cold, in man, to the region of the ulnar nerve at the elbow produces, when the chilling process has reached a certain stage, complete loss of sensibility in the parts to which the nerve is distributed. The irritability of sensitive nerve fibres may also be temporarily suspended by mechanical injuries in their immediate neighborhood, not involving the fibres themselves. Thus a division of certain parts of the white substance in the brain or spinal cord, is known to produce a loss of sensibility in particular regions of the body, which may disappear after a short time, notwithstanding that the wounded fibres remain ununited;[2] and according to the observations of L'Etiévant,[3] section of one branch of a sensitive nerve, beside the persistent anæsthesia of the divided fibres, may also cause a temporary loss of sensibility in neighboring fibres, derived by anastomosis from other branches.

The irritability of sensitive nerve fibres may also be abnormally increased by vascular congestion, or local injuries. The application of cold, or shutting off the supply of blood by the ligature of arteries, may produce in the nerve, before it reaches the stage of insensibility, a condition of unnatural excitement which is indicated by pain, in the parts corresponding to its distribution.

During life the irritability of sensitive nerves is manifested by the evidences of conscious sensation. After death, as in a decapitated animal, it may also be shown to exist, for a certain time, by the reflex actions taking place in the spinal cord or in other parts of the nervous system.

Irritability of Motor Fibres.

The motor nerves are especially convenient for studying the action of nervous irritability, because their excitement has for its result a visible muscular contraction; and this may take place, even when the nerve and its muscle have been separated from the rest of the body. To produce this result, however, as in the case of the sensitive nerves, two conditions are requisite, namely; first, the nerve fibre must preserve its normal irritability; and secondly, the muscular tissue must also be capable of responding to a stimulus by the contraction of its fibres. The laws regulating these two sets of phenomena may therefore be studied in connection with each other.

Mode of exhibiting Muscular Irritability.—This is best shown in the cold-blooded animals, since in them it continues active for a longer time than in the birds and mammalians. A frog's leg is separated from the body of the animal, the skin removed, and the poles of a galvano-electric

[1] Injuries of Nerves and their Consequences. Philadelphia, 1872, p. 59.

[2] Veyssière, Recherches sur l'Hemianæsthésie. Paris, 1874, p. 78.

[3] Traité des Sections Nerveuses. Paris, 1873, pp. 171, 192.

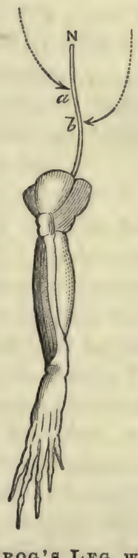
apparatus (Fig. 143, *a*, *b*) applied to the surface of the denuded muscles. A contraction takes place each time the circuit is completed, when the electric discharge passes through the limb. In this case, the stimulus is applied directly to the muscles, and shows that their irritability, or power of contraction under the influence of an exciting cause, does not depend upon their remaining in connection with the nerves or nervous centres. A single muscular fibre, in fact, separated from all neighboring parts, may sometimes be seen to contract under the microscope for a certain time after its removal from the muscular tissue. The muscles will also respond by contraction to various other kinds of mechanical or chemical stimulus, such as pinching, pricking, cauterizing, the contact of hot or cold bodies, or the application of various acid, alkaline, or saline solutions. The most efficient and manageable stimulus, however, is the electric discharge.

Fig. 143.

Frog's Leg, with the poles of a galvanic battery applied to the muscles at *a*, *b*.

Mode of exhibiting Nervous Irritability.—In order to exhibit the irritability of the motor nerve fibres, a frog's leg is prepared, as in the preceding experiment, except that the sciatic nerve is cut off at its point of emergence from the spinal canal, and dissected from the adjacent tissues, so that a considerable portion of it is left exposed, but retaining its connection with the separated limb (Fig. 144). If the two poles of a galvanic battery be now placed in contact with different points (*a*, *b*) of the exposed nerve, and a current allowed to pass between them, at the moment of its passage a contraction takes place in the muscles below. It will be seen that this experiment is altogether different from the one represented in Fig. 143. In that case the electric discharge passes through the muscles themselves, and acts upon them by direct stimulus. Here the current passes only from *a* to *b* through the tissues of the nerve, and acts directly upon the nerve alone; while the nerve, acting upon the muscles by its own special agency, causes in this way a muscular contraction. So long, therefore, as the muscles are in a healthy condition, their contraction, under the influence of a stimulus applied to the nerve, demonstrates the irritability of the latter, and may be used as a convenient measure of its intensity.

Fig. 144.



Frog's Leg, with the sciatic nerve (N) attached. *a*, *b*. Poles of galvanic battery applied to the nerve.

The irritability of a motor nerve continues after death. The knowledge of this fact follows from what has been said with regard to experimenting upon the frog's leg, prepared as above. The irrita-

bility of the nerve, like that of the muscles, depends directly upon its anatomical structure and constitution; and so long as these remain unimpaired, the nerve will retain its vital properties, though respiration and circulation may have ceased. For the same reason, nervous irritability lasts longer after death in the cold-blooded than in the warm-blooded animals. Various artificial irritants may be employed to call it into activity. Pinching or pricking the exposed nerve with steel instruments, the application of caustic liquids, and the passage of galvanic discharges, all have this effect. The galvanic current, however, is the best means to employ for this purpose, since it is more delicate in its operation than the others, and will continue to succeed for a longer time.

The nerve is so sensitive to the galvanic current that it will respond to it when insensible to all other kinds of stimulus. A frog's leg freshly prepared, as above, with the nerve attached, will react so readily when a discharge is passed through the nerve, that it forms an extremely delicate instrument for detecting the presence of electric currents of low intensity, and has been sometimes used for this purpose under the name of the "galvanoscopic frog." It is only necessary to introduce the nerve as part of the electric circuit; and if even a very feeble current be present, it is at once betrayed by a muscular contraction.

Nervous irritability, like that of the muscles, is exhausted by repeated excitement. If a frog's leg, prepared in the manner above described, with the sciatic nerve attached, be allowed to remain at rest in a damp and cool place, where its tissue will not become altered by desiccation, the nerve will remain irritable for many hours; but if it be excited, soon after its separation from the body, by repeated shocks, it begins to react with diminished energy, and becomes gradually less irritable, until at last it ceases to exhibit any further excitability. If it be now allowed to remain for a time at rest, its irritability will be partially restored; and muscular contraction will again ensue on the application of a stimulus to the nerve. Exhausted a second time, and a second time allowed to repose, it will again recover itself; and this may be repeated several times in succession. At each repetition, however, the recovery of nervous irritability is less complete, until it finally disappears altogether, and can no longer be recalled. The irritability of the muscles may be exhausted, in a similar way, by repeated excitement.

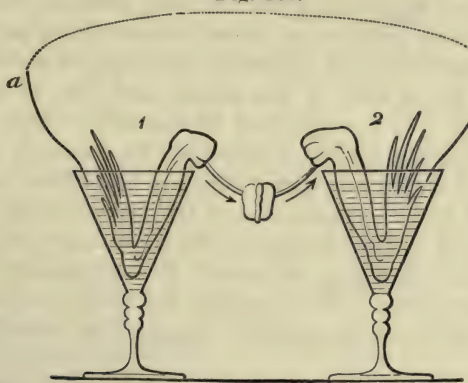
Various circumstances tend to diminish or suspend the irritability of the motor nerve fibres. As in the case of the sensitive fibres, compression, cold, or other similar agencies will depress the power of the muscular nerves, so that they can no longer excite a contraction when subjected to the galvanic current. Severe and sudden mechanical injuries often have the same effect; as where general muscular relaxation, or diminished power of voluntary motion, is produced by any extensive contusion or laceration of one of the limbs. Such an injury produces a general disturbance or *shock*, which affects the entire nervous system,

and destroys or suspends its irritability. The effects of a nervous shock of this kind may frequently be seen in man after railroad accidents, where the patient, though extensively injured, may remain for some hours in a state of unusual muscular debility, and at the same time without the sensation of pain. It is only after reaction has taken place, and nervous irritability has been restored by repose, that the powers of sensation and voluntary motion are re-established.

It is often found, on preparing the frog's leg for experiment as above, that immediately after the limb has been separated from the body and the integument removed, the nerve is destitute of irritability. Its vitality has been suspended by the violence inflicted in the preparatory operation. In a few moments, if kept under favorable conditions, it recovers from the shock, and regains its natural irritability.

Different Action of the Direct and Inverse Currents.—The action of the galvanic current upon the nerves, as first shown by Matteucci, is in many respects peculiar. If the current be made to traverse the nerve in the natural direction of its fibres, namely, from its origin toward its distribution, as from *a* to *b* (Fig. 144), it is called the *direct* current. If it be made to pass in the contrary direction, as from *b* to *a*, it is called the *inverse* current. When the nerve is fresh and exceedingly irritable, or when the galvanic current is of sufficient intensity, a muscular contraction takes place at both the commencement and termination of the current, whether it be direct or inverse. But when the activity of the nerve has become somewhat diminished, or when the current employed is of feeble intensity, contraction takes place only at the *commencement* of *the direct* and at the *termination* of *the inverse* current. This may readily be shown by preparing the two legs of the same frog in such a manner that they remain connected with each other by the sciatic nerves

Fig. 145.



and that portion of the spinal column from which these nerves take their origin. The two legs, so prepared, are placed each in a vessel of water, with the nervous connection hanging between. (Fig. 145.) If the positive pole, *a*, of the battery be now placed in the vessel which holds leg

No. 1, and the negative pole, *b*, in that containing leg No. 2, it will be seen that the galvanic current will traverse the two legs in opposite directions. In No. 1, it will pass in a direction contrary to the course of its nervous fibres, that is, it will be for this leg an *inverse* current; while in No. 2 it will pass in the same direction with that of the nervous fibres, that is, it will be for this leg a *direct* current. It will now be found that at the moment when the circuit is completed, a contraction takes place in No. 2 by the direct current, while No. 1 remains at rest; but at the time the circuit is broken, a contraction is produced in No. 1 by the inverse current, while no movement takes place in No. 2. A succession of alternate contractions may thus be produced in the two legs by repeatedly closing and opening the circuit. If the position of the poles, *a*, *b*, be reversed, the effects of the current will be changed in a corresponding manner.

After a nerve has become exhausted by the direct current, it is still sensitive to the inverse; and after exhaustion by the inverse, it is still sensitive to the direct. It was even found by Matteucci that after a nerve has been exhausted for the time by the direct current, the return of its irritability is hastened by the subsequent passage of the inverse current; so that it will become again sensitive to the direct current sooner than if allowed to remain at rest. Nothing, accordingly, is so exciting to a nerve as the passage of direct and inverse currents, alternating with each other in rapid succession. Such a mode of applying the electric stimulus is that afforded by the Faradic apparatus, in which momentary currents of induced electricity are made to traverse the circuit in two opposite directions in rapid alternation.

The irritability of motor nerves is distinct from that of the muscles. This is shown by the fact that the two properties may be destroyed or suspended independently of each other. When the frog's leg has been prepared and separated from the body, with the sciatic nerve attached, the muscles contract, as shown above, whenever the nerve is irritated. The irritability of the nerve, therefore, is manifested in this instance only through that of the muscle, and that of the muscle is called into action only through that of the nerve. But the action of *woorara* has the power, as first pointed out by Bernard,[1] of destroying the irritability of the nerve without affecting that of the muscles. If a frog be poisoned by this substance, and the leg prepared as above, the poles of a galvanic battery applied to the nerve will produce no effect. But if the galvanic discharge be passed directly through the muscles, contraction takes place. The muscular irritability has survived that of the nerves, and must therefore be regarded as essentially distinct from it.

There are, therefore, two kinds of paralysis: first, a muscular paralysis, in which the muscular fibres themselves are directly affected;

[1] Leçons sur la Physiologie du Système nerveux. Paris, 1858, tome i. p. 199.

and secondly, a nervous paralysis, in which the affection is confined to the nerve fibres, the muscles retaining their natural properties, and being still capable of contraction under the influence of direct stimulus.

Identity of Action in the Sensitive and Motor Nerve Fibres.

The results which are produced by the physiological action of the nerve fibres differ from each other in the two classes to which they belong. The stimulation or excitement of the sensitive fibres produces a sensation, or a sensitive impression in the nervous centre; that of the motor fibres causes contraction of the muscles to which they are distributed. Moreover, if a sensitive nerve or nerve fibre be divided, stimulus applied to its central or attached extremity still excites a sensation, while the application of the same stimulus to its separated or peripheral portion produces no apparent result. On the other hand, if a motor nerve be divided, irritation of its attached extremity, which is still in connection with the nervous centre, is without effect; but irritation of its peripheral portion causes a muscular contraction as before. In other words, the nervous force, in a sensitive nerve, appears to move always in a centripetal direction, that is from without inward; in a motor nerve, on the other hand, in a centrifugal direction, or from within outward. In the natural condition of the parts, also, the excitement of a sensitive nerve never produces directly any other effect than sensation; that of a motor nerve only gives rise to the phenomena of movement.

These facts easily suggest the idea that the two kinds of nerve fibres may be distinct in their properties and modes of action; that the sensitive fibres may be capable of acting only in a centripetal direction and of exciting the phenomena of sensibility; and that the motor fibres can only act from within outward and transmit a special kind of nerve force, adapted to excite muscular contraction.

It is evident, however, that the reasons given above are not sufficient to indicate a difference in the activity of the nerves themselves, but only in the sensible results of its operation. In neither case is there any perceptible effect produced in the nerve, but only in the organ with which it is in connection. When a sensitive nerve is excited, the sensation is perceived in the nervous centre; when a motor nerve is called into activity, the contraction is performed by the muscular fibres at its periphery. It is possible that the condition of the nerve fibres, when in a state of excitement, may be the same in each instance, and that the difference in the effect produced may be due to the different physiological properties of the organs in which they terminate; just as the conducting wire of a galvanic battery may be made to ring a bell or move an index, according to the mechanism with which its poles are connected. There are certain facts which can hardly bear any other interpretation than this, and which lead to the conclusion that the physiological action in the nerve fibres themselves is not essentially different in different kinds of nerves.

1. *The stimulus applied to a nerve, whether sensitive or motor, produces the same effect throughout its entire length.*

In the natural condition of the parts, the impressions made upon the external integument, when they give rise to sensation, are transmitted by the sensitive nerve through its whole course to the nervous centre. There it is perceived as a sensation; and the sensation thus produced is referred by the individual, not to the brain or to any part of the nerve, but to the integument where the nerve originated. If an irritation be applied to the nerve in the middle of its course, the sensation is still perceived as if it came from the same portion of the integument and had travelled through the same distance as before. It is well known that after amputation of a limb in the human subject, if the severed extremity of one of the nerves happen to be compressed or otherwise irritated by the tissues of the cicatrix, or if it be the seat of inflammatory action, many different sensations of pain, movement, heat, or cold, are excited, which are always referred by the individual to the amputated portion of the limb; and patients often assert that they can feel the separated parts as distinctly as if they were still attached to the body. The impression conveyed through the remaining portion of the nerve is the same as if the whole of it were still in existence.

The action of the motor nerves is of a similar kind. A voluntary stimulus, which originates in the brain, passes through the entire length of a motor nerve to reach the muscles and excite their contraction. But if the nerve be divided at any intermediate point, and a galvanic stimulus applied to the peripheral portion, a contraction follows in the same muscles as before. In each case, the physiological effect is produced at the extremity of the nerve fibres; and it seems to make no essential difference in its character from how great a distance it has been transmitted.

So far as yet known, therefore, the nerve fibre, whether sensitive or motor, when its irritability is excited, may be thrown at once into a condition of activity throughout its entire length; the whole nerve assuming a state of *polarity*, analogous to that of a magnetized bar, in which the visible phenomena of attraction or repulsion are manifested only at its extremities, although the whole substance of the bar participates in its magnetic molecular action. When the exciting stimulus, as in the sensitive nerves, is naturally applied at the peripheral extremity, it must necessarily be communicated from without inward; and when it commences at the inner extremity, as in a motor nerve, it must move in a direction from within outward. But nothing thus far shows that it may not be capable of moving in either of these two directions in the same nervous fibre. The following experiments show that this is in reality the case, so far as regards the sensitive nerves.

2. *Sensitive impressions may pass, in the fibres of a sensitive nerve, either from without inward or from within outward.*

This of course never takes place in the natural condition of the parts; but its possibility has been demonstrated, in the experiments of Paul

Bert,[1] by dividing a sensitive nerve and then reversing its position, so that its peripheral extremity is brought into connection with the nerve centres. The end of the tail, in a young rat, was deprived of its integument for a length of five centimetres, and the denuded portion inserted beneath the integument of the back of the same animal. At the end of eight days, when the ingrafted portion had become adherent to the subcutaneous tissues, and had contracted sufficient vascular connection for its support, the tail was amputated at its base, and thenceforward remained attached to the body of the animal only by what was previously its peripheral extremity. In three months the signs of sensibility again began to be manifested when the end of the tail, thus reversed, was subjected to compression; and at the end of six months its sensibility was re-established to an unmistakable degree. The nerves of the tail, which before the operation transmitted sensitive impressions from its point toward its base, afterward transmitted the same impressions from its base toward its point.

There is no evidence, therefore, that nerve fibres are endowed with two different modes of action, one for sensation, the other for motion. In each case the condition of the nerve itself may be of the same nature. But, being thrown into a state of excitement throughout its entire length, it communicates a stimulus to the organ with which it is connected. If this organ be a perceptive nervous centre, the effect produced is a sensation; if a muscle, it results in contraction and movement. These acts cannot be interchanged with each other, because the muscle cannot feel and the nervous centre is incapable of contraction; but they are both indirect effects of the nervous influence, and do not necessarily depend upon any difference in its nature.

Rapidity of Transmission of the Nerve Force.

It is a matter of conscious experience that the operations of the nervous system require a certain time for their accomplishment. The action both of the senses and of the will is exceedingly rapid, but still is not absolutely instantaneous. Between the mental decision to perform a voluntary movement and its actual execution, there is a short but real interval of time, during which the nervous mechanism is called into activity. A certain period also intervenes between the contact of a foreign body with the skin, and our complete perception of its existence and qualities. There is even more or less difference between individuals in the length of time required for the performance of nervous action; the quickness of the senses and the promptitude of the will frequently varying to a perceptible degree. In the case of a voluntary movement, the period consumed in its entire accomplishment may be occupied by three different processes, namely: 1. The act of volition, taking place in the brain; 2. The transmission of the motor impulse, through the spinal cord and nerves, to their peripheral terminations; and 3. The

[1] La Vitalité propre des Tissues animaux. Paris, 1866, p. 12.

excitement of the muscular fibres to a state of contraction. In the case of a sensation, there are also three analogous successive acts, namely: 1. The reception of the impression by the sensitive membrane; 2. Transmission of the stimulus through the nerve fibres inward; and 3. Its perception in the brain as a conscious sensation. It is an important physiological problem to determine the degree of rapidity with which the transmission of stimulus takes place through the nerve fibres in either direction; and it has recently become a matter of practical interest in relation to pathology.

Methods of determining the Rate of Transmission of the Nerve Force.—The measurement of the rate of transmission of the nerve force was first accomplished by Helmholtz,[1] and has since been carried out by a number of different observers with essentially similar results. The principle adopted is in all cases the same. Muscular contraction is excited by a stimulus which passes through two nerves of different length, or through two different lengths of the same nerve; the delay in contraction, when the stimulus passes through the greater of these two distances, gives the time required for its transmission by the intervening nerve fibres.

These experiments were first performed upon nerves and muscles freshly separated from the body in the cold-blooded animals. The gastrocnemius muscle of a frog is prepared, with a portion of the sciatic nerve attached. A galvanic battery with an induction apparatus is also provided, so that the closure of the circuit of the battery will produce an instantaneous electric current in the induction coil. By this means the stimulus of the induced current is first applied to the muscle itself, and the time noted which intervenes between the closure of the circuit and the muscular contraction. This represents the period required for the excitement of the muscular fibres themselves, and was found in the experiments of Helmholtz to be about $\frac{1}{100}$ of a second. If the stimulus be now applied to the nerve in immediate proximity to the muscle, the above interval is not perceptibly altered. But if it be applied to the nerve at a point one, two, or three centimetres distant, a decided retardation is manifested in the muscular contraction; and this retardation becomes greater as the length of the nerve, between the muscle and the point of stimulation, is increased.

The intervals of time in these experiments have been measured by various contrivances, the most successful of which depend upon the use of an automatic registering apparatus, on the principle of that employed by Marey.[2] In this apparatus, a card, with its surface blackened by smoke, moves by clockwork, with uniform velocity, in a horizontal direction. Upon this card the extremity of a diapason or tuning fork, vibrating 500 times per second, traces an undulating line (Fig. 146, *a*) which records the time occupied by the card in moving from one point

[1] Comptes Rendus de l'Académie des Sciences. Paris, 1851, tome xxxiii. p. 262.

[2] Du Mouvement dans les Fonctions de la Vie. Paris, 1868, p. 422.

to another. A straight horizontal line (*b*, is also traced upon the card by the extremity of a slender steel lever, the other end of which forms a part of the galvanic circuit. The closure of the circuit is accomplished by a movement which pushes aside this lever, and thus causes a

Fig. 146.

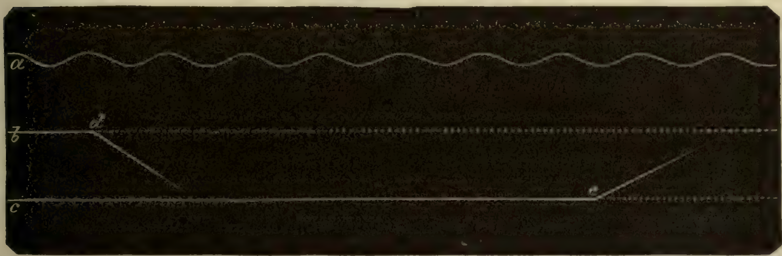


DIAGRAM OF THE REGISTERING APPARATUS, according to the plan of Marey. *a.* Undulating line traced by the diapason, which marks the time consumed by the card in moving from one point to another. *b.* Line traced by the first lever, forming part of the galvanic circuit. *c* Line traced by the second lever, which is moved by the contraction of the muscle. *d.* Deviation of the line *b*, indicating the closure of the galvanic circuit and the stimulation of the nerve. *e.* Deviation of the line *c*, indicating the muscular contraction.

deviation (*d*) in the line traced by its extremity. This deviation registers upon the card the instant of the closure of the circuit, and consequently that of the stimulation of the nerve. The muscle used for experiment is fixed in position, with its tendon attached to a second lever in such a way that any muscular contraction will draw aside its free extremity. This lever traces upon the card a second straight horizontal line (*c*) parallel to the first; and when the muscle contracts, the line is deviated, as at (*e*), by the lateral movement of the lever.

Thus when the experiment has been performed, there are left upon the surface of the card two deviations *d* and *e*, one of which represents the stimulation of the nerve, the other the muscular contraction; and between the two is included a certain interval. The number of undulations in the diapason-trace (*a*), corresponding to this interval, gives the time which has elapsed between the stimulation of the nerve and the contraction of the muscle. In the example shown in Fig. 146, as the interval between the deviations includes 13 simple variations, of which 500 would represent one second, the time occupied is 0.026 of a second. By this means, intervals of time of very short duration may be registered and compared with accuracy.

Subsequently to the experiments upon separated nerves and muscles in the lower animals, investigations of a similar kind were extended to the human subject during life. In the experiments of Baxt,[1] this was done by applying the electrodes to the surface of the skin immediately over the situation of the median nerve, and at varying distances from the muscles to which its fibres are distributed. The nerve was thus

[1] Monatsbericht der Königlichen Preussischen Akademie, April, 1867, and March, 1870.

stimulated at the wrist, at the elbow, and at the upper arm near the lower extremities of the coraco-brachialis and deltoid muscles; the effect of the stimulation being marked by the swelling of the muscles at the ball of the thumb. Here also it was found that the intervening time between the application of the electrodes and the muscular contraction was greater when the stimulus was applied to the nerve at the upper arm, than when applied at the wrist; this increased interval being evidently the time required for the transmission of the nervous impulse from one point to the other. The rate of transmission, as ascertained by these experiments, was found to vary considerably according to the different conditions of cold and warmth; the transmission in the median nerve, when subjected to cold, being sometimes less than one-half as rapid as in the same nerve at a higher temperature.

Finally, in the experiments of Burckhardt,[1] the rate of transmission of the nerve force, for voluntary motion and the acts of conscious sensation in man, has been investigated at considerable length. In these experiments, an automatic registering apparatus was employed, in which the beginning and end of the nervous transmission were marked, as above, by corresponding deviations of a traced line.

Rate of Transmission in the Motor Nerves.—The transmission of the voluntary impulse was measured in Burckhardt's investigations as follows: The galvanic battery and the registering apparatus being properly attached to the person serving for experiment, the signal for the contraction of a particular muscle was given by the sound of a bell connected with the battery. Thus the entire interval registered was that between the sound of the bell and the muscular contraction. A part of this time was consumed in the double act of hearing the sound and producing the volitional impulse. A part was also taken up in the local process of muscular contraction, and only the remainder was occupied in that of nervous transmission. But it is evident that, if, in two different observations, the same signal were used for the contraction of two muscles supplied by different lengths of nerve, the process taking place in the brain and that taking place in the muscle would be alike in both; and any difference in the time observed must be due to the different distances of nerve fibre traversed by the voluntary motor impulse. The muscles employed for this purpose were, in the lower limb, the extensor digitorum communis brevis, tibialis anticus, and semimembranosus, supplied by branches of the sciatic nerve, and the quadriceps extensor cruris, supplied by the anterior crural nerve; in the upper limb, the interosseus externus primus, extensor digitorum communis, flexor digitorum and deltoid, all supplied by branches of the brachial plexus. The result of all the observations upon eight different healthy persons was, that the mean velocity of transmission for the voluntary impulse, in the peripheral nerves of the upper and

[1] Die Physiologische Diagnostik der Nervenkrankheiten. Leipzig, 1875, p. 32.

lower extremities, is a little over 27 metres per second. The minimum velocity was 20 metres, and the maximum 36 metres; but of all the observations, which were thirty in number, twenty-three, or nearly four-fifths, gave results between 26 and 28 metres.

In one instance the rate of movement in the same nerve, for the voluntary impulse and for that excited by galvanism, was tested comparatively, and but little difference was found to exist in the two cases.

According to Burckhardt, also, the rate of transmission does not vary essentially for weak or strong motor impulses; that for a muscular contraction of moderate force passing as rapidly through the nerve as that for contractions of greater power.

Rate of Transmission in the Sensitive Nerves.—The rate of transmission for impressions of conscious sensibility is determined by an analogous method. An irritation or tactile impression is produced upon the skin at varying distances from the nervous centres—as, for instance, upon the foot, the thigh, and the loins; and the instant at which the sensation is perceived is indicated by a movement of the finger. As the time required for the act of conscious perception in the brain and for the voluntary movement of the finger is the same in all cases, the difference between two successive observations is owing to the different lengths of the nerves transmitting the stimulus.

In the investigations of Burckhardt, which were made upon thirteen different individuals, the mean rate of transmission for sensitive impressions through the peripheral nerves was found to be a little less than 47 metres per second; that is, more than one and a half times as rapid as that for voluntary motion. The variations were from a minimum of 20 to a maximum of 73 metres; but in nearly three-fourths of all the observations, the results were confined within a variation of from 40 to 56 metres. The rapidity of transmission varied but little with the increased or diminished intensity of the impression; the difference, on the average, being but little over one per cent.

Rate of Transmission in the Spinal Cord.—The investigations of Burckhardt first indicated a difference between the rate of transmission in the spinal cord and that in the peripheral nerves. This rate was determined for the spinal cord by comparing the time consumed in the passage of a voluntary impulse to the extremities of two nerves, like the sciatic and the ulnar, which emerge from the spinal cord at different points. In this case the voluntary impulse, after leaving the brain, will traverse different lengths of the spinal cord; and as its rate of movement in the peripheral nerves is known, the difference in the time of its entire passage may be easily referred to its increased or diminished rate of movement in the spinal cord. Thus a motor impulse, which calls into action the interosseous muscles of the hand, passes through the cervical portion of the spinal cord, and thence through the lower cervical nerves, the brachial plexus, and the whole length of the ulnar nerve. An impulse which excites contraction in the quadriceps extensor cruris passes through both the cervical and dorsal portions of

the spinal cord, and thence through the lumbar plexus and the anterior crural nerve to the thigh. Consequently its transit through the spinal cord is about three times as long in the second instance as in the first; and its amount of retardation will indicate the rate of transmission in the spinal cord as compared with that in the nerves.

By this means it was found that the transmission of *voluntary motor impulses* in the spinal cord is considerably slower than in the nerves. Its average rapidity was a little over 10 metres per second; the minimum being 8, the maximum 14 metres. Thus the difference in rapidity of transmission through the nerves and the spinal cord becomes very manifest.

TRANSMISSION OF VOLUNTARY MOTOR IMPULSES.

Through the spinal cord	10 metres per second.
" " nerves	27 " "

A comparison of observations on the two opposite sides of the body gave a difference in the rate of transmission, for the right and left lateral halves of the spinal cord, of from 1 to 3 metres per second, always in favor of the left side.

The transmission of *sensitive impressions* through the spinal cord, on the other hand, was found to be nearly as rapid as through the nerves, the average rate being a little over 42 metres per second. A remarkable difference, however, appeared in the transmission of simple tactile impressions and of those which were painful in character. The former are comparatively rapid, as above stated, while painful impressions are communicated through the spinal cord at a much slower rate, amounting on the average to not more than 13 metres per second. Thus the transmission of motor impulses and of tactile and painful impressions respectively, through the spinal cord, is as follows:

RATE OF TRANSMISSION THROUGH THE SPINAL CORD.

For tactile impressions	42 metres per second.
" painful "	13 " "
" motor impulses	10 " "

According to these results the passage of a motor impulse, from the brain to the muscles of the foot, would occupy 0.088 of a second; of which time about one-half would be required for transmission through the spinal cord, and one-half for transmission through the fibres of the sciatic nerve.

Rapidity of Nervous Action in the Brain.—In all the experiments detailed above, an essential part of the nervous operation consists in the hearing of the signal for a voluntary movement and in the act of volition which sets in motion the voluntary impulse. This process, which takes place in the brain, includes both the action of the gray substance of the nervous centres and its transmission by the nerve fibres of the white substance to the origin of the spinal cord. The time thus consumed is ascertained by deducting, from the whole period intervening between the signal given and the contraction of the muscle,

first, the time requisite for the mechanism of muscular contraction, namely, 0.01″, and, secondly, that occupied in the transmission of the impulse through the spinal cord and nerves. Thus if the entire period be 0.220″, and the time required for transmission through the spinal cord and nerves be 0.088″, there remains 0.132″, which is occupied in muscular contraction and in the acts of sensation and volition. Burckhardt's experiments, like those of Helmholtz, fix the time required for local stimulation of the muscle at 0.01″; and he estimates that about an equal interval is necessary for the mechanism of hearing in the external, middle, and internal parts of the ear. The whole process, therefore, of executing a voluntary movement in the foot, at the signal given by a bell, would be divided in time as follows:

TIME OCCUPIED IN EXECUTING A VOLUNTARY MOVEMENT AT A GIVEN SIGNAL.

Mechanism of hearing	0.010″
Acts of perception and volition in the brain . . .	0.112″
Transmission through the spinal cord	0.044″
Transmission through the sciatic nerve	0.044″
Mechanism of muscular contraction	0.010″
	0.220″

It appears that the nervous action in the brain, which represents the operation of the gray substance of the nervous centres, requires a considerably longer time than the transmission of a nervous impulse through the nerve fibres.

The physiological variation in rapidity of any or all the nervous actions above enumerated, in different individuals, causes a difference in the promptitude with which sensible phenomena are perceived and recorded by different observers. This fact was first distinctly noticed in astronomical observations, where it was found that the exact time of the passage of a star across the thread of a transit instrument was differently recorded by different observers; this variation in some cases amounting to as much as one second. Subsequent observations showed that in no case was the time of the transit recorded with absolute accuracy; but that a certain delay always intervened, due to the time necessarily occupied by the nervous mechanism of the observer. This fact was established by imitating the transit of a star by means of a single luminous point moving in a circle with uniform velocity before the field of a telescope. By contrivances similar to those described above, the real instant of the passage of this luminous point across the thread of the telescope field was recorded upon a revolving cylinder, and the observer also marked its passage by similar means. The difference between the real and the observed time represented the "personal error" of the observer. The amount of this error, however, although it varies for different persons, is constant, or nearly so, for the same individual; and, when it has been once ascertained, the results of observation may be so corrected as to approach nearly to absolute precision.

CHAPTER III.

GENERAL ARRANGEMENT OF THE VARIOUS PARTS OF THE NERVOUS SYSTEM.

In man and the vertebrate animals the nervous system may be divided into two secondary systems, or groups of nervous centres with their commissural fibres and nerves. These are, first, the ganglionic or sympathetic, and secondly, the cerebro-spinal system.

Ganglionic System.—The ganglionic or "sympathetic" system occupies mainly the great cavities of the body. It is connected by its nervous branches and ramifications with the internal organs concerned in the functions of nutrition, and more especially with the heart and bloodvessels, which it follows throughout their peripheral distribution. Its especial anatomical character consists in its being composed of numerous separate masses or collections of gray matter, of small size and rounded form, called "ganglia;" from which circumstance the whole ganglionic system takes its name. These ganglia, connected with each other by slender nervous filaments, form a double chain of distinct but associated nervous centres, situated in front of the spinal column throughout the neck and thorax; while in the abdomen they are at certain points fused together into larger and more irregularly shaped masses upon the median line. There are also scattered ganglia about the head, outside the cranial cavity; and everywhere the ganglia or their nerves receive some fibres of communication from the other division of the nervous system. The scattered arrangement of the sympathetic ganglia, and their deep situation among the thoracic and abdominal organs, have hitherto prevented a complete investigation of their functions; and it is doubtful how far any one portion exercises a central or controlling influence over the remainder.

Cerebro-Spinal System.—The cerebro-spinal system, as its name indicates, is made up of the brain and spinal cord as the great nervous centres, with the nerves which originate from them and which are distributed to the voluntary muscles and integument, the organs of special sense, and the commencement and termination of the internal passages of the body. It is especially distinguished by the fact that its deposits of gray substance, instead of being distributed in separate nodules as in the ganglionic system, are collected into two principal continuous masses, the brain and the spinal cord, occupying the cranial and spinal cavities, where they are enveloped and connected by tracts of white substance, which often conceal in an external view the divisions between them.

The cerebro-spinal nervous system is also distinguished by a nearly

complete symmetry of arrangement. The internal abdominal organs are in great measure unsymmetrical, and the corresponding nerves and nervous centres of the ganglionic system present the same want of regularity in their locality and distribution. But while the ganglionic system presides over the internal organs and functions of nutrition, the cerebro-spinal system, on the other hand, is connected with the apparatus of animal life, namely, the organs of sensation and movement by which the living body is brought into relation with the exterior. As these organs, in man and the vertebrate animals, are symmetrically arranged, the cerebro-spinal nervous system presents the same character. Both the brain and the spinal cord are composed of two, right and left, lateral halves; each one of which furnishes the nerves of sensation and motion to the corresponding sides of the body.

Fig. 147.

THE BRAIN AND SPINAL CORD, in profile.

Another striking peculiarity of this part of the nervous system is the mutual *decussation* of the nerve fibres belonging to its two sides. Both the brain and spinal cord have their right and left halves connected by fibres which pass across the median line from one to the other; the different bundles being often interwoven with each other, at the point of transit, in a somewhat complicated manner. This peculiarity extends to the origins of the nerves, which decussate with each other internally; so that the nerve fibres emerging from the right side of the cerebro-spinal mass have their origin from the gray substance of the left lateral half, and those emerging from the left side originate from the gray substance of the right lateral half. The only uncertainty in this respect is whether the decussation be complete or partial; that is, whether all the fibres of a given nerve root be connected with the opposite side of the central mass, or whether a part of them originate from the same and a part from the opposite side. The decussating fibres, in a large number of instances, are anatomically demonstrated. In some remaining exceptions their course is more or less a matter of doubt.

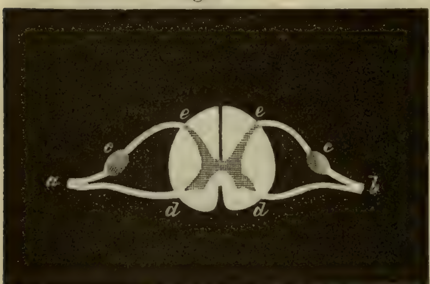
The Spinal Cord is a nearly cylindrical nervous mass, inclosed in the cavity of the spinal canal, commencing by a slightly enlarged extremity

at the brain above, and terminating below in a conical point at the level of the first lumbar vertebra. Its inner portions are occupied by gray substance, which forms a continuous chain of ganglionic matter, running from one extremity of the cord to the other. Its outer portions are composed of white substance, the fibres of which run mainly in a longitudinal direction, connecting its different parts with each other, and forming a communication between it and the brain.

The spinal nerves are given off from the cord at regular intervals and in symmetrical pairs; one pair for each successive portion of the body, their branches being distributed to the integument and muscles of the corresponding regions. In fish and serpents, where locomotion is performed by means of simple, alternating, lateral movements of the spinal column, the cord is nearly or quite uniform in size; or tapers gradually from its anterior to its posterior extremity. But in the other vertebrate classes, where the body is provided with special organs of locomotion as fore and hind limbs, or wings and legs, the cord is increased in size where the nerves of these organs are given off; and the nerves supplying the limbs are larger than those which originate from other parts of the cord. In man, the lower cervical nerves, which form the brachial plexus and supply the arms, and the sacral nerves forming the sacral plexus, which supplies the legs, are larger than those given off in the upper cervical, dorsal, and lumbar regions. The cord itself, furthermore, presents two marked enlargements corresponding with the points of origin of these nerves, namely, the *cervical enlargement*, which is the source of the nerves for the upper extremity, and the *lumbar enlargement*, which gives off the nerves destined for the lower extremity.

A transverse section of the spinal cord shows that it is incompletely divided into right and left lateral halves by an anterior and posterior median fissure; of which the anterior is the wider and penetrates for a comparatively short distance, while the posterior is narrower but extends inward nearly or quite to the centre of the cord. The gray substance in the interior of the cord forms a double crescentic-shaped mass, with the concavities of the crescents turned outward. As these masses are found at all parts of the cord, they have in reality the form of elongated ribbons or bands of gray substance, one on each side, running continuously throughout the length of the cord. The two are united with each other by a transverse band of gray substance, known

Fig. 148.



TRANSVERSE SECTION OF THE SPINAL CORD, showing its central mass of gray substance, and the roots of the spinal nerves.—*a*, *b*. Spinal nerves of right and left sides. *d*. Origin of anterior root. *e*. Origin of posterior root. *c*. Ganglion of posterior root.

as the "gray commissure," in the centre of which is a narrow longitudinal canal, the "central canal," but little over 0.2 millimetre in diameter, and lined internally with epithelium.

The anterior and posterior portions of gray substance, in each lateral half of the cord, are called the anterior and posterior *horns*. Immediately in front of the gray commissure is a transverse band of white substance, the "white commissure" of the cord.

The spinal nerves originate from the cord on each side by two distinct sets of fibres, forming the anterior and posterior roots. The anterior root (Fig. 148, *d*) passes out from the surface of the cord near the extremity of the anterior horn of gray matter. The posterior root (*e*) originates at a point corresponding with the posterior horn of gray matter. Both roots are composed of a considerable number of fibres, united with each other in parallel bundles. The posterior root is distinguished from the anterior by the presence of a small rounded mass of gray matter, or ganglion, with which it is incorporated and through which its fibres pass. The two roots unite with each other soon after leaving the cavity of the spinal canal, and mingle their fibres in a common trunk.

The white substance of each lateral half of the spinal cord is thus divided into three portions or "columns;" so called because the nerve fibres composing them run, for the most part, parallel with each other, in a longitudinal or vertical direction. The portion which is included between the anterior median fissure and the origin of the anterior nerve roots is the *anterior column;* that between the anterior and posterior nerve roots is the *lateral column;* while that between the posterior nerve roots and the posterior median fissure is the *posterior column.* As the posterior median fissure penetrates deeply into the substance of the cord, quite down to the gray substance, the posterior columns appear entirely separated from each other in a transverse section; but the anterior median fissure is more shallow and stops short of the gray matter, so that the anterior columns are connected with each other by the white commissure above mentioned.

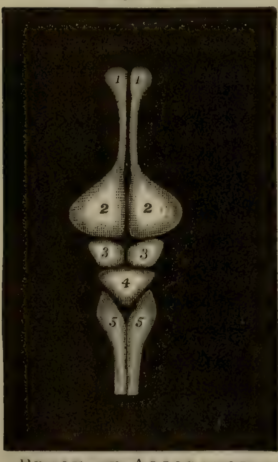
The *brain*, or "encephalon," is that portion of the cerebro-spinal system contained in the cranial cavity. It forms a more or less rounded mass of nervous matter, consisting, as in the spinal cord, of right and left lateral halves which remain connected with each other by their central parts. In man and the higher vertebrate animals, it presents, above and behind, two principal divisions, namely, the cerebrum and cerebellum, which are composed externally of a convoluted layer of gray substance, these two divisions together forming at least nineteen-twentieths of the whole encephalon; while beneath them is a smaller portion composed externally of white substance, like the spinal cord, and forming the communication between the cord below and the brain above. This inferior portion is called the "isthmus," and comprehends the medulla oblongata, the tuber annulare, and the peduncles of the cerebrum. Beside, however, the portion visible externally, there are, in

each of these divisions, various deep-seated deposits of gray substance, which are concealed by the overlying parts.

The construction of the brain, as a whole, may therefore be represented by considering it as a double series of nervous centres or deposits of gray substance, of varying size and position, connected with each other and with the spinal cord by transverse and longitudinal tracts of white substance. The number and relative importance of these nervous centres, in different kinds of animals, depend upon the perfection of the bodily organization in general, and more especially upon the development of the functions and capacities connected with particular parts of the nervous system. In the inferior classes, as fish and reptiles, the brain is more simple in its anatomical characters; while it becomes successively more complicated in birds, quadrupeds, and man.

In *fish* and *reptiles* the different nervous centres of the brain are so distinctly separated, and of such moderate size, that they are frequently designated as "ganglia." In the brain of the alligator (Fig. 149) there are five pairs of these ganglia, arranged one behind the other in the cavity of the cranium. The first of these are two rounded masses ($_1$), lying just above and behind the nasal cavities, which distribute their nerves upon the olfactory membrane. These are the *olfactory ganglia.* They are connected with the rest of the brain by two long and slender commissures, the "olfactory commissures." The next pair ($_2$) are somewhat larger and of a triangular shape, when viewed from above downward. They are termed the "hemispherical ganglia," or the *hemispheres*, and correspond to the "cerebrum" in the higher classes. Immediately following them are two quadrangular masses ($_3$) which give origin to the optic nerves, and are therefore called the *optic ganglia.* They are termed also the "optic tubercles;" and in some of the higher animals, where they present an imperfect division into four nearly equal parts, they are known as the "tubercula quadrigemina." Behind them is a single triangular collection of nervous matter ($_4$), the *cerebellum.* Finally, the upper portion of the cord, just behind and beneath the cerebellum, is seen to be enlarged and spread out laterally, so as to form a broad oblong mass ($_5$), the *medulla oblongata.* It is from this latter portion of the brain that the pneumogastric or respiratory nerves originate, and its ganglia are therefore sometimes termed the "pneumogastric" or "respiratory" ganglia.

Fig. 149.



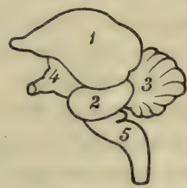
BRAIN OF ALLIGATOR.—1. Olfactory ganglia. 2. Hemispheres. 3. Optic tubercles. 4. Cerebellum. 5. Medulla oblongata.

It will be seen that the posterior columns of the cord, as they diverge laterally, to form the medulla oblongata, leave between them an open

space, which is continuous with the posterior median fissure of the cord. This space is known as the "fourth ventricle." It is partially covered in by the backward projection of the cerebellum, but in the alligator is still somewhat open posteriorly, presenting a kind of chasm or gap between the two lateral halves of the medulla oblongata.

The successive ganglia which compose the brain, being arranged in pairs as above described, are separated from each other on the two sides by a longitudinal median fissure, which is continuous with the posterior median fissure of the spinal cord. In the brain of the alligator this fissure appears to be interrupted at the cerebellum; but this is due to the incomplete development of the lateral portions of this organ, as compared with its middle. The same peculiarity is to be seen in birds and in most quadrupeds; while in man the lateral portions of the cerebellum are so highly developed as to project, on each side, above the level of its central part, and the longitudinal median fissure, accordingly, appears complete throughout.

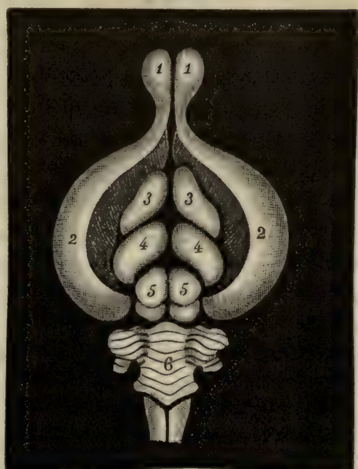
Fig. 150.



BRAIN OF PIGEON—Profile view.—1. Cerebrum. 2. Optic tubercle. 3. Cerebellum. 4. Optic nerve. 5. Medulla oblongata.

In *birds* the hemispheres, or cerebrum, are of comparatively larger size, and partially or completely conceal the optic tubercles in a view taken from above. The cerebellum is well developed in this class, and presents on its surface a number of transverse foldings or convolutions by which its gray substance is considerably increased in quantity. The cerebellum extends so far backward as to completely cover the medulla oblongata and the fourth ventricle.

Fig. 151.



BRAIN OF RABBIT, viewed from above.—1. Olfactory ganglia. 2. Hemispheres of the cerebrum, turned aside. 3 Corpora striata. 4. Optic thalami. 5. Tubercula quadrigemina. 6. Cerebellum.

In *quadrupeds* the cerebrum and the cerebellum attain a still greater size as compared with the remaining parts of the brain. There are also two other collections of gray substance on each side, situated in the inferior part of the hemispheres, anteriorly to the tubercula quadrigemina. These are the "corpora striata" in front, and the "optic thalami" behind. These bodies are frequently designated by the name of the "cerebral ganglia," since they are collections of gray matter which occupy the lower and central parts of the cerebrum, and intervene between the tracts of white

substance, coming up from below, and those which continue upward to the convolutions of the hemispheres. The cerebellum, in the quadrupeds, is somewhat enlarged by the increased development of its lateral portions, and shows an abundance of transverse convolutions. It conceals from view the fourth ventricle and the greater part of the medulla oblongata.

In the more highly developed quadrupeds, the cerebral hemispheres increase in size so as to cover more or less completely the olfactory ganglia in front and the cerebellum behind. Their surface also becomes covered with numerous convolutions, which are mainly longitudinal or curvilinear in direction, instead of being transverse as in the cerebellum.

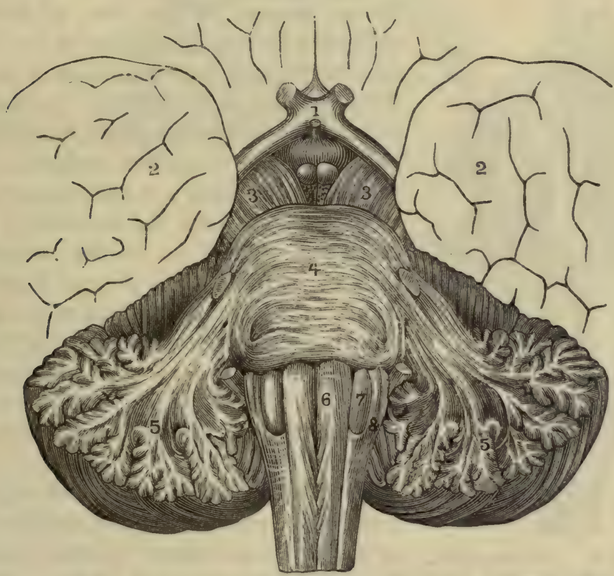
In *Man* the development of the cerebral hemispheres reaches its highest point, so that they preponderate completely over all the other nervous centres in the cranial cavity. In the human brain, accordingly, when viewed from above, there is nothing to be seen but the convex convoluted surface of the hemispheres; and even in a posterior view they conceal everything but a portion of the cerebellum. The remaining parts, which are concealed by the cerebrum and cerebellum, participate, however, in the structure of the entire encephalon, and form, as in the lower animals, a series of associated nervous centres and connecting tracts of nerve fibres.

As the spinal cord passes upward into the cranial cavity, it enlarges, by a kind of lateral expansion, to form the medulla oblongata. This portion of the cerebro-spinal axis is distinguished from the cord below, not only by its external form, but also by the somewhat different arrangement of its gray and white substance. The gray substance, which in the cord presents on each side, in front and rear, the projections of the anterior and posterior horns, recedes, in the medulla oblongata, more and more in a backward direction, and becomes accumulated in a nearly single mass at its posterior surface. At the same time, the masses of white substance on each side of the posterior median fissure, which in the cord are called the "posterior columns," diverge from each other at an acute angle, leaving between them the space of the fourth ventricle, and assume the name of the *restiform bodies.* They become continuous with the inferior peduncles of the cerebellum, and send some of their fibres, in a radiating direction, into the white substance of the cerebellum, to terminate in the gray substance of its convolutions. The floor of the fourth ventricle, thus exposed by the divergence of the posterior columns, is formed by the gray substance of the medulla oblongata, which is accordingly continuous with that of the cord, although it has a different position and a different form.

Viewed in front, the medulla oblongata presents two longitudinal eminences of white substance, one on each side of the median line, the *anterior pyramids*, which take the place of the anterior columns of the cord. At their commencement below, the anterior pyramids are narrow, but grow wider as they ascend. At their lower portion they exhibit a

remarkable *decussation*, easily seen by gently separating the sides of the anterior median fissure, formed by distinct bundles of white substance crossing the median line obliquely, from below upward and from side to side. Thus the right anterior pyramid is formed of fibres which come from the left side of the cord, and the left anterior pyramid of those which come from the right side of the cord.

Fig. 152.



Medulla Oblongata and Base of the Brain in Man—Anterior view.—1. Decussation of the optic nerves. 2, 2. Middle lobes of the cerebrum. 3, 3. Crura cerebri. 4. Tuber annulare. 5, 5. Lateral lobes of the cerebellum. 6. Anterior pyramid. 7. Olivary body. 8. Restiform body. (Hirschfeld.)

Immediately outside of the pyramids, in a lateral direction, are two elongated oval masses, the *olivary bodies*, which consist externally of white substance, but internally contain each a distinct thin convoluted layer of gray substance, resembling in miniature the convolutions of the cerebrum. The olivary bodies are, therefore, special deposits of gray substance in the anterior portion of the medulla oblongata, superadded to the rest and not continuous with that of the spinal cord.

At the upper limit of the medulla oblongata is the *tuber annulare*, so called because it forms a ring-like protuberance at this part of the base of the brain. Superficially, when viewed in front, it consists of transverse bundles of white substance, containing fibres passing over, in an arched form, from one side of the cerebellum to the other, and decussating with each other at the median line. Where they cross the tuber annulare these fibres constitute the "pons Varolii;" at the two sides, where they pass backward to the cerebellum, they form the "middle peduncles of the cerebellum."

In its deeper parts, the tuber annulare contains longitudinal tracts of white substance, passing upward from the medulla oblongata toward the cerebrum. The continuation of the anterior pyramids in front, and the remainder of the longitudinal bundles of the medulla oblongata behind, pass into and through the substance of the tuber annulare, where they are mingled with an irregular diffused deposit of gray substance. From the upper border of the tuber annulare, the longitudinal tracts of white substance emerge in the form of two thick, obliquely diverging, bundles of nerve fibres, the *crura cerebri*, or peduncles of the brain. They are joined posteriorly by other longitudinal bundles coming from the cerebellum, known as the "anterior peduncles of the cerebellum," which are the organs of communication between the cerebellum and the cerebrum. The fibres of the crura cerebri, thus constituted, then plunge into the substance of the two collections of gray matter known as the "cerebral ganglia," namely, the corpora striata and optic thalami; thus making a connection between these ganglia and the medulla oblongata and spinal cord below.

Fig. 153.

MEDULLA OBLONGATA, TUBER ANNULARE, AND CRURA CEREBRI.—The superficial and deep transverse fibres of the tuber annulare have been cut away, showing the continuation of the longitudinal fibres in its interior. 1. Decussation of the optic nerves. 2. Crus cerebri. 3. Lateral portion of the pons Varolii. 4. Anterior pyramid. 5. Olivary body. (Hirschfeld.)

Finally, from the outer and upper portions of the cerebral ganglia, the nerve fibres of the white substance radiate in all directions, following a more or less curvilinear course from within outward, until they reach the gray substance of the convolutions at the surface of the hemispheres. The cerebral convolutions of the two sides are also united by the transverse fibres of the corpus callosum.

The entire brain may, therefore, be considered as a symmetrical series of nervous centres connected with each other and with the spinal cord by longitudinal tracts of white substance. They occur in the following order: 1. The olfactory lobes, of small size and concealed beneath the anterior portion of the brain; 2. The cerebral hemispheres, surrounding and covering the remaining parts by their lateral and posterior extension; 3. The corpora striata, 4. The optic thalami, and 5. The tubercula quadrigemina, occupying the central portion of the base of the cerebrum, and resting upon 6, the crura cerebri; 7. The tuber annulare; 8. The cerebellum, and 9. The medulla oblongata. Of the collections of gray substance just enumerated, the cerebrum and cerebellum only are convoluted externally, the others being either smooth and rounded or irregular in form.

It is not to be supposed that the nervous communications between the successive deposits of gray matter are necessarily of so simple a character as those represented in Fig. 154. This is only a diagram, representing the general fact of the longitudinal connection existing

Fig. 154.

Diagramatic Section of Human Brain; showing the situation of the nervous centres and the longitudinal tracts of white substance.—1. Olfactory lobe. 2, 2. Convolutions of the cerebral hemispheres. 3. Corpus striatum. 4. Optic thalamus. 5. Tubercula quadrigemina. 6. Crura cerebri. 7. Tuber annulare. 8. Cerebellum. 9. Medulla oblongata.

between the spinal cord and the different parts of the encephalon. It is by no means certain that all or any of the fibres of the cord run continuously through the medulla oblongata, the tuber annulare, and the cerebral ganglia, to the gray matter of the convolutions. On the contrary, careful examination of successive microscopic sections by the best observers have failed to show such a direct continuity. It appears more probable that the fibres coming from the spinal cord terminate in the medulla oblongata, and that other fibres originating from the gray matter of the medulla pass upward, partly to the cerebellum and partly to the corpora striata and optic thalami; while other fibres still, originating from these ganglia, diverge thence to form the connection between them and the cerebral convolutions. According to this view, the longitudinal tracts of white substance consist of nerve fibres which are interrupted in their course by the nerve cells of different deposits of gray matter, so that an impression or impulse conveyed from one to the other is not the same throughout its course, but is modified by the action of the nervous centres which successively receive and transmit it.

Each portion of the cerebro-spinal axis has its right and left halves connected with each other by transverse commissures, and sends out nerves, containing motor and sensitive fibres, to corresponding regions of the body. The spinal cord supplies the integument and muscles of the neck, trunk, and extremities. The medulla oblongata sends out motor and sensitive nerves to the muscles of the head and face, and to the skin and mucous membranes of the same region; while it also sup-

plies nerves of a special character to the mucous and muscular coats of the pharynx, œsophagus, and stomach, and to those of the organs of respiration in the neck and thorax. From the medulla oblongata and the inferior or central parts of the brain, are also supplied the nerves destined for the organs of special sense.

In every region of the cerebro-spinal system, the two functions of sensibility and motion are associated with each other by means of the gray substance of the nervous centres. In the spinal cord the gray substance is continuous and of nearly the same configuration throughout. In the different parts of the brain it presents itself under the form of more or less distinct deposits, of varying form and size. In either of these parts a reflex action may take place independently of those beyond, and calling into operation the special functions of the nervous centre involved. But a nervous action may also pass through the entire series, by the longitudinal connections of the cord, medulla oblongata, tuber annulare, and cerebral ganglia, and thence through the radiating fibres of the white substance to the cortical layer of the cerebral convolutions. This layer may be regarded as a sort of concave mirror, where the impressions coming from without are finally received and reflected, in the form of conscious sensation and intelligent voluntary acts; the whole nervous mechanism of the cerebro-spinal system being thus called into operation at the same time.

CHAPTER IV.

THE SPINAL CORD.

THE spinal cord is that part of the cerebro-spinal system which is contained within the spinal canal, and which sends its nerves to the muscles and integument of the trunk and limbs. It consists externally of white substance, forming longitudinal tracts of nerve fibres, the continuations of which make connection with those of the brain above; and internally of gray substance arranged in two symmetrical bands occupying the central portions of its right and left lateral halves. It is so constituted, therefore, as to act in a double capacity: First, as an organ of nervous communication between the brain and the external parts; and secondly, as an independent nervous centre, with endowments and functions of its own.

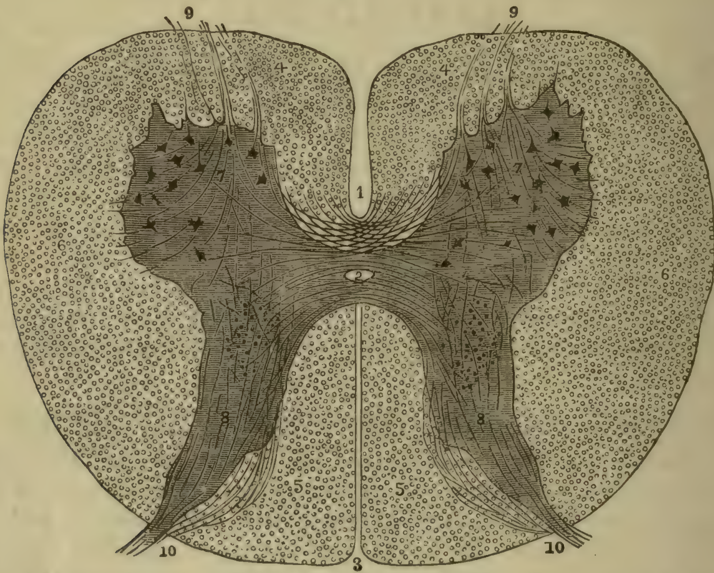
Arrangement of Gray and White Substance in the Spinal Cord.

The mutual relations of the gray and white substance form the necessary basis for a complete physiological anatomy of this part of the nervous system. The connections of the nerve fibres with the cells of the gray substance and with various parts of the longitudinal columns, as well as those of the different nerve cells with each other, are the most important for this purpose. It has not yet been possible to make out these connections with certainty for all parts of the cord; but much has been accomplished in this respect by the examination of microscopic sections made in various directions, after hardening the tissues of the cord in alcohol or in weak solutions of chromic acid or potassium bichromate, and by making the fibres and cells more distinct by means of staining preparations. With regard to the relative proportions, in different parts of the cord, of its two constituent elements, it is evident, as shown by Kölliker and Gerlach, that the gray substance is increased in quantity at the situation of the cervical and lumbar enlargements, and that the white substance, on the other hand, diminishes gradually, from its upper to its lower extremity. This fact corresponds with the known physiological relations of the cord; namely, that by its gray substance it acts as a nervous centre for the corresponding regions of the body; and also that the fibres of its white substance form communications between the parts above and the spinal nerves which are given off below.

The Gray Substance.—The gray substance in the spinal cord, as elsewhere, consists of a mixture of nerve cells and nerve fibres, of which the nerve cells are the peculiar and distinctive element. They are all

"multipolar" cells; that is, they send out several prolongations in various directions, transverse, longitudinal and oblique, most of which are abundantly subdivided and terminate in minute ramifications, while a single one frequently continues its course for a long distance undivided,

Fig. 155.



Transverse Section of the Spinal Cord; lower cervical region.—1. Anterior median fissure; immediately behind it are seen the decussating fibres of the white commissure. 2. Central canal, situated in the middle of the gray commissure. 3. Posterior median fissure. 4, 4. Anterior columns of white substance. 5, 5. Posterior columns. 6, 6. Lateral columns. 7, 7. Anterior horns of gray substance. 8, 8. Posterior horns. 9, 9. Anterior nerve roots. 10, 10. Posterior nerve roots.

and assumes the appearance of an axis cylinder. They vary in form and size in different parts of the gray substance. The most remarkable of these cells are situated in the *anterior horns*, where they are distinguished by their large size, being, according to the measurements of Kölliker, from 67 to 135 mmm. in diameter, the largest known cells in the nervous system. They are arranged in two or three more or less distinct groups near the extremity and outer portion of the anterior horns. Beside these there are found scattered everywhere in the gray substance, but more abundantly in the *posterior horns*, nerve cells which are much smaller in size than the preceding, but of similar form and provided with similar branching prolongations. The anterior and posterior horns are not therefore absolutely distinguished from each other by the character of their nerve cells, but only by the relative proportions of their size and numbers; since a few cells of comparatively large size are found in the posterior horns, and the smaller ones exist in both situations.

The nerve fibres of the gray substance are, in general, of much smaller diameter than those of the white substance, but otherwise present the same anatomical characters. Most of them run in a horizontal transverse, antero-posterior, or radiating direction. They consist, first, of fibres which have penetrated into the gray substance from the anterior and posterior roots of the spinal nerves; secondly, of fibres which cross the median line in the gray commissure, from one side of the cord to the other, thus forming a commissural connection between the two lateral halves of the gray substance; and, thirdly, of fibres which run in a great variety of directions with regard to each other, and of which the origin and terminations are unknown.

The White Substance.—The white substance of the spinal cord consists of nerve fibres, the large majority of which run in a longitudinal direction, forming tracts or "columns," designated, according to their situation, by the names of the *anterior*, *lateral*, and *posterior* columns of the cord. In transverse sections of the cord which have been properly hardened, the longitudinal fibres are readily distinguished by their presenting the circular outline of a minute cylinder cut across; while those which are horizontal or oblique are seen in profile for a longer or shorter distance in the preparation.

The anterior, lateral, and posterior columns consist almost exclusively of longitudinal fibres. But at the bottom of the anterior median fissure there is a band of white substance, the fibres of which run horizontally across from the inner portions of each anterior column to the opposite side of the cord. This is called the *white commissure of the cord;* but the name is not entirely appropriate, since its fibres do not form a connection between exactly corresponding parts on the right and left sides. According to both Kölliker and Gerlach, the fibres which pass across at the median line from the right anterior column spread out in the gray substance of the left anterior horn; and those coming from the left anterior column spread out in the gray substance of the right anterior horn. The transverse fibres, accordingly, of the white commissure connect the right and left anterior columns respectively with the gray substance of the opposite side of the cord.

Counting the transverse fibres, therefore, of both the gray and the white commissures, it may be said that there is a direct bilateral connection, by means of communicating nerve fibres, between the right and left halves throughout the length of the cord; but it is not possible to determine, with precision, the exact origin or termination of the individual fibres by which this connection is made.

Connection of the Spinal Nerve-roots with the Spinal Cord.—The fibres of the *anterior* roots of the spinal nerves are distinguished from those of the posterior by their relatively larger size; but on penetrating into the white substance of the cord, their diameter is diminished, and they assume all the characters of the central nerve fibres. They then pass inward, in a horizontal or oblique and backward direction, and reach the *gray substance of the anterior horn.*

The exact termination of the nerve fibres in the gray substance of the cord is a matter of much importance, but which is not yet fully elucidated. The strong probability is that some of the fibres of the anterior nerve roots are directly connected with radiating nerve cells in this locality by means of the long axis-cylinder processes of these cells; but the most accomplished and careful microscopists have found it impossible to actually see this connection. Its probability rests upon the facts that, first, the long processes of the nerve cells in the anterior horns closely resemble, as their name indicates, the axis-cylinder of the nerve fibres; and, secondly, these processes are often seen, in horizontal or antero-posterior vertical sections, to pass forward toward the origin of the anterior root fibres, and emerge, in company with them, from the gray into the white substance of the cord.[1] Beside these fibres, however, others, forming a part of the anterior nerve roots, pass distinctly, according to Kölliker, from the gray substance of the anterior horn into the white commissure, and thence, crossing the median line, into the anterior column of white substance on the opposite side; while others, radiating backward and outward, may be seen to emerge from the external border of the gray substance, and to join the longitudinal fibres of the lateral column on the same side.

Thus it is certain that the immediate connection of all the fibres of the anterior nerve roots is with the gray substance of the anterior horn; but some of them pass subsequently to the anterior column of the opposite side of the cord, others to the lateral column of the same side.

The *posterior* roots are distinguished from the anterior, first, by the generally smaller size of their nerve fibres; secondly, by the presence of the ganglia, known as the "spinal ganglia," or the ganglia of the spinal nerve roots. The gray substance of these ganglia contains nerve cells which are distinguished from those of the spinal cord by not possessing ramified prolongations. They present, however, often one, sometimes two or more, pale, unbranched axis-cylinder processes, which subsequently become continuous with medullated nerve fibres, running outward with the other nerve fibres toward the periphery. These ganglia therefore give origin to additional nerve fibres, which afterward form part of the trunk of the spinal nerve. The fibres of the posterior nerve roots, on the contrary, coming from the spinal cord, according to Kölliker, only traverse the gray matter of the ganglion, without making any anatomical connection with its substance.

The fibres of the posterior roots, on entering the spinal cord, between its posterior and lateral columns, pass into the posterior horns of gray matter; after which some of them change their direction and become longitudinal, still remaining in the gray substance, others become trans-

[1] Kölliker, Eléments d'Histologie Humaine. Paris, 1868, p. 343. Gerlach, in Stricker's Manual of Histology, Buck's edition. New York, 1872, pp. 636, 637.

verse, passing into both the gray and white commissures, while others lose themselves in the gray substance of the posterior and even of the back part of the anterior horns.

The connection of the anterior and posterior root fibres of the spinal nerves with the cord is therefore not exactly the same; but they both, so far as known, first reach the gray matter, where a portion of them terminate, or at least escape further observation, while the rest partly become longitudinal on the same side, and partly cross over to the opposite side of the spinal cord.

Transmission of Motor and Sensitive Impulses in the Spinal Cord and Nerves.

The experimental methods adopted for determining the functions of different parts of the nervous system are twofold; first, by applying an artificial stimulus to the nerve or nervous tract, and observing the effect which is produced; secondly, by dividing or destroying it, and seeing what nervous function is abolished in consequence of the operation. In the peripheral parts of the nervous system, and in those generally which serve as simple organs of transmission, both these methods yield definite and positive results. In the central parts, they are sometimes complicated by the peculiar properties or the mutual reactions of the gray and white substance.

Motor and Sensitive Transmission in the Spinal Nerves and Nerve Roots.—If the spinal canal of a living animal be opened, and a mechanical or galvanic stimulus be applied to the anterior root alone of a spinal nerve, the effect of this irritation is a convulsive movement of the part to which the nerve is distributed. The muscular contraction is immediate, involuntary, and instantaneous in duration; and is repeated with mechanical precision each time the stimulus is applied. It is usually unaccompanied by any indication of sensibility, and is evidently a direct result of the excitement of the nerve fibres of the anterior root. This root is therefore said to be "excitable," because its irritation excites a movement in the corresponding parts.

Furthermore, if the anterior root of a spinal nerve, under the same circumstances, be cut across, the remaining nervous connections being left untouched, the result is an immediate and total paralysis of voluntary movement in the muscles to which that nerve is distributed. At the same time, the power of sensibility is undiminished, and the animal is still capable of feeling the contact of foreign bodies, or a galvanic current applied to the skin, as before. If the anterior roots of a series of spinal nerves be thus divided, as, for example, those of all the lumbar and sacral nerves on one side, the above effect will be produced for an entire corresponding region of the body, and the whole posterior limb on that side will lose the power of voluntary motion while retaining its sensibility. This is not due to any loss of the physiological properties of either the nerve or the muscles, since irritation of the nerve or nerve root, outside the point of section, still produces muscular contraction as

before. All these facts prove that the path by which impulses for voluntary motion pass, from the brain and spinal cord to the muscles, is exclusively the anterior root of the spinal nerve.

On the other hand, if the posterior root be irritated, by pinching, pricking, or galvanism, a sensation is produced, more or less acute according to the amount and quality of the irritation applied. This sensation, when of a certain intensity, is accompanied by movements. But these movements are general and not necessarily confined to the part to which the nerve is distributed; and if the corresponding anterior root have been previously divided, this part will remain motionless, while muscular contractions continue to be produced elsewhere. The movements which follow irritation of the posterior root, accordingly, are not produced directly by its influence, but are caused indirectly by the reaction of the nervous centres. The only immediate result of irritation of a posterior nerve root is a sensation, and this root is therefore said to be "sensitive."

Furthermore, if the posterior root be divided, the consequence is a loss of the power of sensation in the corresponding region of the body. Here also the effect is simply to cut off the medium of communication between the integument and the nervous centres; since irritation of that part of the divided nerve which is still attached to the spinal cord produces a sensation as before. Thus the channel of communication for sensitive impressions, in this part of the nervous system, is exclusively the posterior root of the spinal nerve.

But just beyond the situation of the spinal ganglia, the two roots unite to form the trunk of the spinal nerve. Here, the fibres of the anterior and those of the posterior root become intimately mingled, and inclosed within the neurilemma in such close juxtaposition that they can no longer be separately irritated by artificial means. They pass, still associated in this manner, into the branches and subdivisions of the nerve; and only finally separate from each other at its terminal ramifications, where the sensitive fibres are distributed mainly to the integument and the motor fibres to the muscles.

The trunk and branches of a spinal nerve, therefore, outside the spinal canal, contain both sensitive and motor fibres, and it is consequently said to be a "mixed" nerve. It is both excitable and sensitive, since its artificial irritation causes at the same time sensation and convulsive movement; and if it be divided, this injury is followed by the loss of both sensibility and voluntary motion in the corresponding parts. It is also important to remember that, in all these instances of section of the trunk, or branches, or anterior or posterior roots of a spinal nerve, the consequent loss of sensibility or motion is permanent while the injury lasts; and the nervous functions are not restored until the divided nerve fibres have reunited, and have again acquired their natural continuity of texture. This shows that the suspension of functional activity is directly due to the division of the nerve fibres, and is not produced by the sympathetic action of other parts.

Motor and Sensitive Transmission in the Spinal Cord.—The simplest fact determined, in this respect, both by experimental research and pathological observation, is that the spinal cord is the exclusive organ of communication between the brain, on the one hand, and the external organs of sensation and motion, on the other; since if it be divided by a transverse section, or compressed by fractured bone, or disorganized by diseased action at any part of its length, the result is a complete loss of voluntary motion and sensibility in the muscles and integument below the point of injury. The general nervous function, performed by the cord as a whole, is therefore easily and completely demonstrated, and is not subject to any doubtful interpretation.

But the precise path which is followed by the motor and sensitive impulses respectively in different parts of the spinal cord is much less easy of determination than in the two sets of nerve roots. The fibres of the nerve roots pass directly to the gray matter in the interior of the cord; and their subsequent course has not been completely followed by microscopic examination. The white substance of the cord, at least in the lateral columns, is partly formed of fibres which come from the nerve-roots; but the greater part of both anterior, lateral, and posterior columns may consist of fibres which originate in the gray matter, and thus form secondary tracts of communication between it and the brain. The close juxtaposition and continuity of texture between the gray substance and the various columns of white substance in the spinal cord give it a more or less complicated structure; and the investigation of the functional endowments of its different parts has yielded results which are less simple and uniform than in the case of the nerves and the nerve roots. The methods and objects of the investigation, however, are the same in both instances; and are intended to ascertain the following points, namely, first, what parts of the spinal cord are found to be sensitive or excitable under the application of an artificial stimulus? and secondly, what parts act as the natural channels of transmission for the two functions of sensation and motion? The latter of these questions is the more important in a purely physiological point of view; but the former is also of consequence as a guide in experimental research, and also for the explanation of many pathological phenomena.

I. *What parts of the Spinal Cord are sensitive or excitable under the influence of artificial stimulus?*

When the spinal canal is opened in the living animal, the first portions of the cord which present themselves for examination are the *posterior columns.* The irritation of these columns by artificial stimulus, according to the united testimony of all observers, produces evident signs of sensibility in the animal. It is also found by experimenters generally that this sensibility is most marked in the immediate neighborhood of the attachment of the posterior nerve roots, while at the greatest distance from this point, namely, at the inner edge of the posterior columns, on each side of the median line, their sensibility may be

nearly absent. It is evident that the sensibility of the posterior columns is largely due to the presence of fibres of the posterior nerve roots, which may be included in the irritation, and many of which traverse the outer portion of the posterior columns horizontally in their passage toward the gray matter. The only discrepancy on this subject is in regard to the question whether the fibres of the nerve roots are the only sources of sensibility for the posterior columns, or whether the longitudinal fibres of the columns themselves are also sensitive. According to some authors (Van Deen, Brown-Séquard, Poincaré), the posterior columns have no sensibility of their own, but only what is due to that of the posterior nerve roots; since if these roots be torn out, irritation of the posterior columns no longer produces any perceptible sensation. In the experiments of Schiff and Vulpian, on the other hand, the posterior columns, after being divided by a transverse section, and then separated from the adjacent parts for a distance of several centimetres in front of the point of section, still indicate the existence of sensibility when subjected to irritation. Irritation of the posterior columns, like that of sensitive tracts generally, produces also movements in various parts; but these movements are reflex in character, and are simply the signs of an irritation communicated to the nervous centres.

Sensibility also exists, according to Vulpian, in that portion of the *lateral columns* which is contiguous to the outer edge of the posterior columns, and to the line of attachment of the posterior nerve roots. But as the irritation is applied to points farther forward, the signs of sensibility in the lateral columns rapidly diminish, and soon disappear altogether. In all these parts, of both posterior and lateral columns, the sensibility, as found by all observers, is most marked, or even exclusively situated, in their superficial portions; and experimenters are also generally agreed that the *gray substance* of the cord, throughout, is destitute of sensibility to the application of any ordinary artificial stimulus.

Whatever minor points, therefore, may remain in doubt, the principal fact is unquestioned, namely, that the posterior parts of the spinal cord, consisting of the posterior columns and the adjacent parts of the lateral columns, are sensitive to external irritation, especially at their surface; and accordingly inflammation of the meninges, or other diseased action in this locality, may be accompanied by painful irritation of the spinal cord. The irritation thus produced is still more liable to cause pain, on account of the attachment at the surface of the cord of the posterior nerve roots, which are themselves acutely sensitive.

The properties shown by the *anterior columns* on the application of artificial stimulus are, on the whole, quite different from those of the posterior columns. There is some difference in the results obtained in this respect by different experimenters. This difference mainly consists in the fact that, according to the large majority (Magendie, Longet, Bernard, Brown-Séquard, Vulpian, Flint), irritation of the anterior columns produces convulsive movement in the parts below; while

others (Calmeil and Chauveau) have found these columns quite inexcitable, and incapable of causing muscular contraction. But in such instances experiments with a positive result are much more decisive than those which are merely negative, since the natural excitability of the anterior columns might be temporarily suspended by the operation of opening the spinal canal, or other incidental conditions; but nothing of this kind could confer upon them a property which they did not naturally possess.

Vulpian has shown[1] that, if in the living animal the spinal cord be divided transversely, and both posterior and lateral columns, together with the anterior and posterior nerve roots, separated from it for a distance of four or five centimetres below the point of section, leaving this portion of the cord to consist of the anterior columns and the gray substance only, irritation of the anterior columns, thus isolated, will still produce convulsive movement in the parts below.

There can be no doubt, accordingly, of the excitability of the anterior columns. This excitability, which produces simple convulsive movements in the parts below, is also in most instances unaccompanied by pain or other evidences of sensibility. The absence of pain, in cases where the convulsive action is well marked, has been especially noticed by Flint,[2] and is also mentioned by various other writers.

The sensibility of these parts which has sometimes been observed is comparatively slight in degree, and is frequently altogether suspended or abolished by the opening of the vertebral canal and the exposure of the spinal cord.

The *lateral columns* are also excitable in their anterior portions, near the attachment of the anterior nerve roots; while as we approach their posterior portions, this direct excitability, according to Vulpian, diminishes in degree, and gradually gives place to the phenomena of sensibility characteristic of the posterior parts of the cord.

The anterior, lateral, and posterior columns of the cord are not therefore absolutely limited and distinguished from each other by their physiological properties. The fibres of the anterior and posterior nerve roots pass in horizontally between the longitudinal fibres of the adjacent columns; but both the anterior and lateral columns, on each side of the anterior nerve roots, are excitable and produce movement on being irritated, and both the posterior and lateral columns, near the entrance of the posterior nerve roots, are endowed with sensibility. Inflammatory or other irritation of the meninges, over any part of the anterior aspect of the cord, may accordingly cause convulsive movements in the regions situated below the diseased point; and it is possible that either pain alone or convulsions alone may be the symptoms of inflammatory irritation of the posterior or anterior portions of the cord respectively. But it is most frequently the case that the morbid action extends more

[1] Système Nerveux. Paris, 1866, p. 360.
[2] Physiology of Man; Nervous System. New York, 1872, p. 276.

or less to both regions, and the disturbances of sensibility and motion are both present at the same time, or at different periods in the progress of the disease.

II. *What parts of the Spinal Cord are the natural channels of transmission for sensation and movement?*

This question cannot be settled by the experiments which consist in applying an artificial stimulus to the various parts of the cord. Such experiments can only determine the sensibility or excitability of a nervous tract, but not its function as a channel of transmission. A part of the spinal cord might be sensitive to direct external irritation, and yet the natural impulses of sensation, coming from the peripheral nerves, might follow a different route. On the other hand, a part might be perfectly capable of transmitting the nervous impulses of sensation or of motion, received from the corresponding nerve fibres, and yet might not itself be either excitable or sensitive. In the peripheral nerves and the nerve roots, the two sets of properties coexist. The nerve fibres of the posterior roots, which transmit sensation, are themselves sensitive; and those of the anterior nerve roots, which transmit the power of motion, are also excitable. But although these properties are connected in the nerves and nerve roots, they are not necessarily so in the nervous centres; and investigation shows that in the spinal cord they are often independent of each other.

The only method of ascertaining what path is followed, in the spinal cord, by the sensitive and motor impulses respectively, is to divide or destroy, in successive experiments, different portions of the cord, and to observe which of these injuries is accompanied by the loss or preservation of sensation or voluntary movement. Even these experiments are not always as decisive in the spinal cord as in the nerves and nerve roots; for the reason that the different parts of the white and gray substance influence each other, and are sometimes affected by sympathetic action. If the division of one of the columns of the spinal cord be followed by a continuance of the power of sensation, we know that column cannot be the natural channel for sensitive impressions. But if, on the other hand, it be followed by immediate loss of sensibility, we cannot be sure, in this case, that the column in question is really the organ of transmission; because the loss of sensibility may be temporary, and due to the shock inflicted upon neighboring parts of the cord. Nothing is more common, in experiments on the nervous system, than to see a paralysis of sensation or motion, more or less complete, follow directly upon the injury of a particular part, and yet these symptoms disappear within a few hours or days, although the injury to the nerve substance may remain for a much longer period. The immediate effect, in these cases is not due directly to the division of the injured nerve fibres, but to their sympathetic reaction upon neighboring parts of the nervous centre. The most decisive experiments, accordingly, upon the spinal cord, for determining the channels of transmission for sensation and

motion, are those in which these functions have remained, notwithstanding the section of certain parts of the cord.

By investigating in this way the nervous channels for *sensation* in the spinal cord, the first fact which is demonstrated in such a manner as to be generally accepted, is that after division of the posterior columns of white substance the power of sensibility is undiminished, and the animal continues to feel impressions made upon the integument of the corresponding parts. This result, which was obtained by several of the older experimenters, is fully confirmed by the observations of Brown-Séquard[1] and Vulpian.[2] The posterior columns therefore are not the channels for ordinary sensitive impressions, notwithstanding they have themselves a certain degree of sensibility. The converse of this experiment, namely, transverse division of all parts of the spinal cord excepting the posterior columns, as performed by the same observers, is followed by complete loss of the power of sensation.

On the other hand, if both the anterior and lateral columns of white substance be divided, leaving only the posterior columns and the gray substance, sensibility is preserved; and Brown-Séquard has varied the mode of procedure by dividing both anterior, lateral, and posterior columns in the same animal at different levels, one above the other, so that the continuity of the cord as a whole is preserved, but all the longitudinal tracts of white substance are divided, leaving only the gray substance uninjured. In this case sensibility is preserved, although diminished in intensity.

The transmission of sensitive impressions, therefore, takes place through the gray matter. This substance, which is itself insensible to direct irritation, forms the medium of communication between the peripheral fibres of the sensitive nerves and the brain above. It is not known whether this communication be made by nerve fibres running continuously through the gray substance in a longitudinal direction, or by successive connections of the nerve cells.

With regard to the channels for *voluntary motion* in the cord, the posterior columns, it is certain, take no direct part in the transmission of these impulses, since after their complete section the power of voluntary motion remains unimpaired; and if all the remaining parts of the cord be divided, according to the observations of Brown-Séquard, leaving the posterior columns untouched, voluntary motion is entirely lost. Further experiments by the same author on the anterior and lateral columns and the gray substance of the anterior horns lead to the conclusion that, for the transmission of the voluntary impulses from the brain to the muscles of the body and limbs, *both the white and gray substance* of the anterior half of the cord must be in a state of integrity; since section of either the white substance alone or of the gray sub-

[1] Physiology and Pathology of the Central Nervous System. Philadelphia, 1860, p. 19.

[2] Système Nerveux. Paris, 1866, p. 373.

stance alone is followed by almost complete paralysis of the parts below the level of the injury. In the dorsal region, injury of the anterior columns produces a greater amount of paralysis than that of the lateral columns; in the cervical region, on the other hand, this relation is reversed, the lateral columns taking a more important part in voluntary transmission than the anterior.

It is evident, accordingly, that in the spinal cord the transmission of sensitive and motor impulses does not take place with the same simplicity as in the nerves and nerve-roots. The various nervous tracts, as well as the white and the gray substance, are associated in such a manner as to make of the cord a single organ, more or less complicated in structure, which cannot be separated, so far as our present knowledge extends, into completely independent parts.

Crossed Action of the Spinal Cord.

The spinal cord, as a medium of nervous communication between the brain and the external parts, exerts a crossed action. That is, the sensitive impressions received by the integument on one side of the body are conducted through the cord to the opposite side of the brain; and the voluntary motor impulses which originate on one side of the brain pass to the nerves and muscles on the opposite side of the body. This is established both by experiments upon animals and by pathological observations in man; since injury or disease situated upon the right side of the brain is known to cause paralysis, both of sensation and voluntary motion, on the left side of the body, and *vice versâ.* These two nervous functions may be paralyzed either together or separately, according to the locality and extent of the injury to the brain substance; but when the paralysis is distinctly confined to one side of the body, the alteration of nervous tissue upon which it depends is found after death to be seated upon the opposite side of the brain.

The crossing or decussation of the motor and sensitive tracts, from side to side, takes place in the following manner:

Decussation of the Motor Tracts.—It may be said, in general terms, that the transmission of voluntary motor impulses, in the spinal cord itself, takes place continuously upon the same side. That is, if a transverse section of one lateral half of the cord be made at any point in the lumbar, dorsal, or cervical region, a paralysis of voluntary motion is produced upon the same side for all parts situated below the level of the injury. This observation, which was first made by Galen, has been confirmed by all subsequent experimenters. But in the cervical region, the lateral columns gradually preponderate in importance, as the organs of transmission for voluntary motion, over the anterior columns; and on approaching the level of the medulla oblongata, their fibres pass in a direction forward and inward, until they reach the inner and anterior part of the cord. At the medulla oblongata, these fibres cross the median line, as distinct bundles of considerable size passing obliquely upward, to form the anterior pyramids of the opposite side. This

constitutes the so-called "decussation of the anterior pyramids;" and beyond this point the longitudinal fibres of the medulla oblongata continue their course toward the peduncles of the brain and the cerebral ganglia above. Thus the crossing of the tracts for voluntary motion is completed in the lower half of the medulla oblongata. Injury of one lateral half of the brain above this situation causes muscular paralysis on the opposite side of the body; injury of one lateral half of the spinal cord below it causes paralysis on the same side of the body.

These are the general results obtained from both pathological observation and physiological experiment; and they evidently point to the medulla oblongata as the principal or exclusive seat of the bilateral decussation of the channels for voluntary motion. At the same time it is shown, by mircroscopic examination, that this is not the only spot where an anatomical intercharge of fibres takes place between the two lateral halves of the spinal cord. On the contrary, a decussation of fibres exists everywhere, throughout the length of the cord, from left to right, and *vice versâ*, at the situation of the "white commissure," at the bottom of the anterior median fissure; the right anterior column constantly receiving fibres from the left side of the cord, and the left anterior column from the right side of the cord. This continuous decussation is concealed from view externally, and is only discoverable by means of transverse microscopic sections; while that at the level of the anterior pyramids is easily visible, owing to the size of the decussating bundles and their oblique direction.

The anatomical distinction between the two sets of decussating fibres may answer to a corresponding difference in their physiological action; and the decussation at the white commissure may be connected with the reflex action of the cord, or with the simultaneous action of its two opposite sides. It is certain that this commissure does not take part in the transmission of voluntary impulses; since in the celebrated experiment of Galen,[1] "if the spinal cord be divided by a longitudinal section, from above downward, in the median line," so as to separate its two lateral halves from each other, this operation is not followed by loss of motion either on one side or the other. This result has also been obtained by Brown-Séquard[2] in the lumbar region, voluntary motion being retained in both the posterior limbs. On the other hand, as shown by the same observer, a longitudinal section of the medulla oblongata alone in the median line, so as to divide the decussating fibres of the anterior pyramids, produces complete loss of voluntary movement in all the limbs at once.

Decussation of the Sensitive Tracts.—The sensitive impressions, conveyed from the integument to the nervous centres, undergo, like the motor impulses, a complete bilateral decussation by the time they arrive

[1] De Administrationibus Anatomicis. Liber viii. cap. vi.

[2] Physiology and Pathology of the Central Nervous System. Philadelphia, 1860, p. 33.

at the upper part of the medulla oblongata; since lesions of the brain above this point cause a diminution or loss of sensibility on the opposite side of the body.

But while the tracts for voluntary motion have a continuous or unilateral course in the spinal cord itself, and decussate only or principally at the level of the anterior pyramids, those for sensation in great measure cross from side to side at successive points throughout the length of the spinal cord. This is shown by the fact that a transverse section of one lateral half of the spinal cord, which paralyzes motion on the same side with the injury, causes, on the contrary, a loss of sensation on the opposite side; while sensibility remains upon that side of the body where the section of the cord has been made. Thus if the lateral section of one-half the spinal cord be made at the lower end of the dorsal region on the right side, the right hind leg is paralyzed of motion but retains its sensibility; the left hind leg, at the same time, retains its power of motion but loses its sensibility. Furthermore, the sensibility of the parts is not only retained on the side of the section, but is even exaggerated in a very perceptible manner; so that an impression upon the skin is perceived on that side more acutely than before the section.

These results, which were partially obtained by several of the older experimenters, were first distinctly brought out by Brown-Séquard. According to his experiments, the phenomena are so complete as to imply an entire crossing of the sensitive tracts in the spinal cord. Other observers have found the appearances not so decisive; Vulpian, among others, maintaining that the loss of sensibility on the opposite side, after section of a lateral half of the cord, is never complete but only partial, and that the sensitive impressions conveyed through the gray matter may even continue to pass, after one lateral half of the cord has been divided in the dorsal, and the other in the cervical region, by two sections placed at a considerable distance from each other.

It is certain, however, that after section of one lateral half of the cord the phenomena which indicate a crossing of the sensitive tracts are distinctly marked. We have repeated this experiment, and have found that after such a section, in the dog, in the dorso-lumbar region, the difference in the effects produced upon sensation and motion on the two sides is very striking. Sensibility is either lost or very much diminished upon the opposite side, while upon the same side with the section, where there is complete muscular paralysis, the sensibility remains and is increased in intensity. On the opposite side, there is power of motion with diminution or loss of sensibility; on the same side, there is hyperæsthesia with loss of voluntary motion.

What is the cause of the local hyperæsthesia, after section of one lateral half of the spinal cord? This is an instance of the indirect influence exerted upon the nervous centres by injury of any part of their substance. After transverse division of one-half of the cord, not only are its motor and sensitive fibres cut off, causing paralysis of motion

on the same side and paralysis of sensibility on the opposite side, but the gray substance is irritated in the neighborhood of the section and is thrown into a state of unusual activity. The sensitive fibres of the posterior nerve roots on the same side pass into this gray substance below the point of section, and thence make communication with the opposite side of the spinal cord and the brain. The irritation of the gray matter thus causes an increase in the intensity of the nervous impressions coming from the side of the injury and an apparent hyperæsthesia of the integument on that side. For this purpose it is not necessary to make a complete section of all the lateral parts of the cord; since Brown-Séquard has found that division of the posterior columns alone will cause hyperæsthesia, more or less pronounced; and according to Vulpian, the same effect may be produced by simply pricking with a pointed instrument the posterior or lateral parts of the cord on one side.

Another experiment is much relied on by Brown-Séquard to demonstrate the crossing of the sensitive tracts in the spinal cord. According to him, if the spinal cord be divided, in the lumbar region, by a longitudinal section in the median line, so as to separate its two lateral halves from each other without further injury, the operation is followed by complete loss of sensibility in both hind legs. This result by itself would not be decisive, since such an operation might readily cause a temporary suspension of sensibility, owing to the shock inflicted on the spinal cord as a whole; but it is of much value when taken in connection with the fact that after this operation, while sensibility is lost, the power of voluntary movement, on the contrary, is retained in both the posterior limbs.

Finally, instances in the human subject, where a lesion of one side of the spinal cord is accompanied by loss of voluntary motion on the same side and loss of sensibility on the opposite side, below the seat of the disease, confirm the results derived from experiments on animals. The decussation of both motor and sensitive tracts is completed at the medulla oblongata; but below this point the cord acts as a conductor for motor impulses going to the muscles on the same side of the body, and for sensitive impressions coming from the integument of the opposite side.

Various forms of Paralysis, from lesions of the Cerebro-spinal Axis.—In consequence of disease or injury in different parts of the cerebro-spinal axis, a variety of symptoms may be produced affecting sensation and voluntary motion. The two most simple forms of paralysis from this cause are, first, "paraplegia," or paralysis of the entire lower portion of the body and inferior limbs; and secondly, "hemiplegia," or paralysis of one lateral half of the body, and of one or both limbs on the corresponding side.

I. In *Paraplegia*, the injury affects the whole substance of the spinal cord at a particular level, and the result is loss of sensation and voluntary motion on both sides, for the whole of that part of the body supplied with nerves which originate at or below the level of the injury.

The seat of the lesion in the spinal cord is determined by the line at which paralysis of sensation and motion begins in the external parts. If the lesion occupy the lumbar portion of the cord, the legs and the pelvic regions are paralyzed and insensible, while the arms and remaining parts of the trunk retain their feeling and power of motion. If it be in the dorsal region, a corresponding part of the abdomen and thorax is also deprived of sense and movement; and if situated in the middle cervical region, it produces at the same time paralysis and insensibility of both upper and lower extremities, together with that of the chest and intercostal muscles. A paralysis of this kind, affecting the arms and intercostal muscles, is more dangerous than that of the legs alone; because a slight extension of the lesion above the middle cervical region will paralyze the fibres of origin of the phrenic nerves, and produce death by stoppage of respiration.

In complete paraplegia, sensation and motion are both abolished in the affected parts; because the injury or disease, when sufficient to destroy one of these nervous functions, almost necessarily reaches those portions of the cord which preside over the other. But in slight or incomplete cases, either sensibility or movement may be more or less affected, according as the lesion is more or less advanced in different parts of the thickness of the cord.

II. In *Hemiplegia* of the simplest form, there is loss of sensation and voluntary motion in the right or left arm and leg, the limbs on the other side of the body remaining uninjured. Sensibility and the power of movement are also lost in the integument and muscles of the chest and abdomen on the corresponding side. It is, therefore, a complete paralysis of one lateral half of the body; the affection being usually exactly limited by the median line, both in front and rear. In these cases the paralysis is due to some lesion within the cavity of the cranium, on the opposite side, and above the decussation of the anterior pyramids; namely, in the upper part of the medulla oblongata, the crura cerebri, the cerebral ganglia, or the hemispheres. It appears to be most frequently seated in the cerebral ganglia or the hemispheres.

In hemiplegia from this cause, the loss of sensibility and of the power of motion, though occupying the same half of the body, are not necessarily equal in degree. According to Hammond,[1] when the cause of the difficulty is a cerebral hemorrhage, they are rarely present to the same extent. If the lesion be situated lower down, in the crus cerebri or the tuber annulare, they would be more likely to resemble each other in degree.

When hemiplegia is due, on the other hand, to a lesion of the spinal cord on one side, the paralysis of motion is on the same side of the body, and that of sensibility on the opposite side. A number of these cases have been collected by Brown-Séquard, in most of which it was ascertained that the injury was seated in the lateral half of the cord corresponding to the paralysis of motion.

[1] Diseases of the Nervous System. New York, 1871, p. 77.

Action of the Spinal Cord as a Nervous Centre.

So far as the spinal cord is concerned in the phenomena of sensation and voluntary motion, it acts as a medium of communication between the brain, where consciousness and volition reside, and the integument and muscles of the external parts. Its complete division accordingly at any point destroys this communication, and suspends the nervous functions dependent upon it; so that the commands of the will are no longer transmitted to the muscles below, and the individual is incapable of perceiving impressions made upon the integument of the paralyzed parts. But after such an operation motion is not altogether abolished in the body and limbs; and impressions conveyed by the sensitive nerve fibres, though no longer perceived by the individual, are still capable of producing an effect, and of exciting a reaction in the organs of movement. These phenomena, which take place without the intervention of the brain, are produced by the action of the spinal cord as a nervous centre, and are due to the independent properties of its gray matter.

Reflex Action of the Spinal Cord.—If a frog be decapitated, and allowed to remain at rest for a few moments, until the depressing effects of the shock upon the nervous system have passed off, movements can readily be excited in either the anterior or posterior limbs. If the skin of one of the feet be irritated by pinching with a pair of forceps, or by immersing it in a weak acidulated solution, the leg is immediately drawn upward toward the body, as if to escape the source of irritation. If the stimulus applied be of slight intensity, the corresponding leg only will move; but if it be more severe in character, motion will often be produced in the corresponding limb on the opposite side, or even in all the extremities at once. These phenomena may be repeated a great number of times, until the irritability of the nervous system has been exhausted, or until some structural change has taken place in the tissues.

Two important peculiarities are noticeable in the movements thus produced after decapitation:

First, they are never spontaneous; but are only excited by the application of an external stimulus. The decapitated frog, if left to itself, always remains perfectly motionless, in a nearly natural attitude, but without any tendency to alter its position. Each application of a stimulus causes a movement, after which the limbs again assume a condition of quiescence until a repetition of the stimulus calls out a new movement.

Secondly, the muscular action thus manifested is not produced by a stimulus directly applied to the muscles themselves. The stimulus is applied to the integument of the foot, and the muscles of the leg and thigh are contracted in consequence. This shows that both sensitive and motor nerve fibres take part in the action. The sensitive fibres distributed to the integument first receive the impression and convey it

inward; after which the motor fibres transmit an outward stimulus to the muscles in a different part of the limb. Even the other limbs, as already mentioned, may be set in motion by an irritation applied to the integument of one.

Furthermore, the nervous action is not transmitted, in these cases, directly from the integument to the muscles; it passes through the spinal cord, which thus forms a necessary link in the chain of communication; for if the posterior limb be left uninjured, while its connection with the cord is severed by dividing the sciatic nerve in the cavity of the abdomen, no further action can be excited, and the limb remains motionless whatever irritation be applied to the integument.

Lastly, if the spinal cord itself be destroyed by the introduction of a stilet into the spinal canal, this also puts an end to the phenomena, and irritation of the integument will no longer produce a muscular reaction. After that, the muscles can only be excited to contraction by a stimulus applied directly to themselves, or to their motor nerves.

All these facts show that the phenomena in question are due to the reflex action of a nervous centre, in which three different nervous elements take part; namely, first, the sensitive nerve fibres, conveying an impression inward from the integument; secondly, motor nerve fibres, transmitting a stimulus outward to the muscles; and, thirdly, a nervous centre which intervenes between the two, and in which the reflex action is accomplished. The nervous centre, in this instance, is the gray substance of the spinal cord.

It is evident, accordingly, that consciousness is not a necessary accompaniment to the reception of sensitive impressions by a nervous centre; and that a motor impulse may also originate in a nervous centre without the act of volition. The reflex action of the spinal cord takes place without either consciousness or volition; and yet it is completely efficient, and produces muscular contraction at once on the application of a stimulus to the skin.

Diminution or Increase of Reflex Action in the Cord.—The reflex action of the spinal cord, like other forms of nervous activity, may suffer a temporary depression, or even total suspension, by any shock or injury to the system at large. The operation of separating the head from the trunk in the frog will often be followed, for a few moments, by an interval of complete nervous paralysis, in which no phenomena of reaction can be obtained. Even injuries in which the nervous centres are not directly interested, such as the opening of the abdomen and the removal of the abdominal organs, may produce a similar temporary effect. In some instances the duration of this period of depression is very short, so as to be almost imperceptible; in others it lasts for several minutes. After it has passed off, the reflex irritability of the cord returns to its natural condition, and, if the cord itself have been wounded or divided, may even be perceptibly increased in intensity.

It is for this reason that the reflex action of the cord often seems to be more vigorous and prompt in the frog after the removal of the head,

or the transverse division of the cord itself at its upper part. The wound of the nervous substance induces an increased excitability of its gray matter, in consequence of which sensitive impressions of a moderate character produce a more energetic muscular reaction. This is shown by the observations of Türck, Bernard, and Vulpian, in which, after a section of one lateral half of the cord, the posterior leg on that side is withdrawn more rapidly from an acidulated solution than the other; and in which the reflex action of the cord, in decapitated animals, becomes more and more marked, for the posterior limbs, in consequence of successive transverse sections made from before backward, in the cervical and lumbar regions.

The reflex action of the cord may also be increased by poisonous substances. Strychnine is the most efficient in this respect, and produces very rapidly an exalted condition of irritability in the spinal cord, in consequence of which a slight irritation of the skin is followed by excessive muscular reaction. If a frog be simply decapitated and left in repose for a short time, the reflex action of the cord manifests itself, as usual, in a distinct but moderate degree. Slight irritations have no perceptible effect, and the pinching of the skin in one hind foot usually causes retraction of that limb only. But if a solution of strychnine be injected underneath the skin, at the end of ten or fifteen minutes, when absorption has taken place, the reflex irritability of the cord is found to be exaggerated in a very marked degree. The animal still remains motionless if undisturbed; but the slightest irritation applied to the skin, the contact of a hair or feather, or the jar produced by striking the table upon which it is placed, will often be sufficient to throw it into violent convulsive action, in which all the limbs take part. As these effects are produced in the decapitated animal, no influence can be attributed to the action of the brain. Strychnine, accordingly, is a poison which acts directly upon the spinal cord by increasing its excitability, and by thus causing convulsive movements in consequence of slight external irritation.

Similar results are known to follow from wounds or injuries either of the cord itself or of peripheral parts of the nervous system. Brown-Séquard has found[1] that in Guinea-pigs a section of one lateral half of the spinal cord sometimes produces, after a few weeks, such a condition of the nervous centres that the animal becomes epileptic, and that epileptiform convulsions of a very intense character may be excited by pinching the skin of part of the face and neck, on the side corresponding with the lateral section of the cord. The phenomena of tetanus in man, following wounds of the peripheral nerves, are also of a reflex convulsive character. The tetanic spasm is often, if not always, excited by an external cause; but this cause is so slight that in the healthy condition it would have no perceptible effect. The accidental movement of the bedclothes, the shutting of a door, the passing of a carriage in the

[1] Researches on Epilepsy. Boston, 1857.

street, or even a current of air upon the skin, may be sufficient to throw the muscular system into severe spasmodic action. The reflex irritability of the spinal cord may, therefore, be increased or diminished by various causes acting upon it from without.

Reflex Action of the Cord in Warm-blooded Animals and in Man.—In the frog, as well as in other cold-blooded animals, the reflex action of the spinal cord lasts for a comparatively long time after decapitation or the stoppage of the circulation; continuing sometimes, if the animal be kept in repose and sufficiently cool and moist, for twenty-four hours or even longer. In the warm-blooded animals, it disappears much more rapidly; and it must be sought for, if at all, within a very short time after death, since a nearly constant supply of blood is essential in these animals to a continuance of the physiological action in every part of the nervous system. If artificial respiration be kept up, however, so as to maintain the circulation, the reflex action of the cord will continue to manifest itself, independently of the brain; and the same thing may be accomplished, by dividing the spinal cord in the lower cervical or upper dorsal region below the origin of the phrenic nerve. The animal then continues to breathe by means of the diaphragm; and although deprived of both sensibility and voluntary motion in the posterior limbs, movements of the leg are produced by pinching the skin of the foot.

Robin has observed the phenomena of reflex action of the cord, after decapitation, in man, in the case of an executed criminal whose body was subjected to examination. The reflex muscular contractions were produced about one hour after the execution.[1] "While the right arm was lying extended in an oblique position by the side of the trunk, with the hand about 25 centimetres distant from the upper part of the thigh, I scratched with the point of a scalpel the skin of the chest at the areola of the nipple, for a space of 10 or 11 centimetres in extent, without making any pressure upon the subjacent muscles. We immediately saw a rapid and successive contraction of the great pectoral muscle, the biceps, probably the brachialis anticus, and lastly the muscles covering the internal condyle."

"The result was a movement by which the whole arm was made to approach the trunk, with rotation of the arm inward and half-flexion of the forearm upon the arm; a true defensive movement, which brought the hand toward the chest as far as the pit of the stomach. Neither the thumb, which was half bent toward the palm of the hand, nor the fingers, which were half bent over the thumb, presented any movements."

"The arm being replaced in its former position, we saw it again execute a similar movement on scratching the skin, in the same manner as before, a little below the clavicle. This experiment succeeded four times, but each time the movement was less extensive than before; and

[1] Journal de l'Anatomie et de la Physiologie. Paris, 1869, p. 90.

afterward the scratching of the skin over the chest produced only contractions in the great pectoral muscle which hardly stirred the arm."

The neck had been severed, in the above case, at about the level of the fourth cervical vertebra.

The reflex action may also be seen very distinctly in the human subject, in certain cases of disease of the spinal cord. If the upper portion of the cord be disintegrated by inflammatory softening, so that its middle and lower portions lose their natural connection with the brain, paralysis of voluntary motion and loss of sensation ensue in all parts of the body below the seat of the anatomical lesion. Under these conditions, the patient is incapable of making any muscular exertion in the paralyzed parts, and is unconscious of any injury done to the integument in the same region. But if the soles of the feet be gently irritated with a feather or with the point of a needle, a convulsive twitching of the toes will often take place, and even retractile movements of the leg and thigh, altogether without the patient's knowledge. Such movements may frequently be excited by simply allowing the cool air to come suddenly in contact with the lower extremities. We have repeatedly witnessed these phenomena, in a case of disease of the spinal cord, where the paralysis and insensibility of the lower extremities were complete. Many similar instances have been reported by various authors.

Physiological Action of the Spinal Cord, as a Nervous Centre, during health.—The physiological character of the reflex action of the spinal cord, as it takes place in the healthy condition, is not easily brought under observation. In animals, unless the head be removed or the spinal cord separated from the brain, the reflex and voluntary movements are liable to be confounded; and in man during health the phenomena of sensation and volition are so prominent, as to conceal or obscure those which are performed independently of the consciousness and the will. Nevertheless, the latter are exceedingly important, and many of them in almost constant operation.

The general character of the reflex actions of the spinal cord is that they tend unconsciously to the *defence or preservation* of the body. This character is even seen in the simple experiments performed upon the decapitated frog. If the frog in this condition be suspended in the air by its anterior extremity, the posterior limbs hang downward in a perfectly relaxed condition. On pinching the integument of a foot, or immersing it in acidulated water, the limb is drawn upward by contraction of its flexor muscles, and the result of this movement is a withdrawal of the foot from the source of irritation. When the muscles relax, the limb lengthens until the foot again touches the irritating liquid, when it is again drawn up; and so on, until the irritability of the cord is so far diminished, or accustomed to that particular stimulus, that it no longer reacts. In this case, therefore, it is not all the muscles of the leg and thigh which are thrown into activity by irritating the skin, but only the flexors, which tend to withdraw the foot from the

irritation to which it is subjected. When an irritation is applied to the skin on the side of the trunk, it is common to see a hind foot applied to the irritated spot, as if to protect if from a repetition of the stimulus; and in some instances the adaptation of reflex movements to accomplish a definite result is very marked. This cannot be attributed to any faculty of perception belonging to the spinal cord; since we know, from pathological cases in man, that when the cord is separated from the brain by disease or injury, the parts below are left absolutely without conscious sensibility or power of volition. The character of the movement produced therefore depends directly upon the anatomical structure of the limbs and the nervous mechanism of the spinal cord. In the case of reflex action observed by Robin in a decapitated criminal, the effect of gentle irritation of the skin over the front of the chest was a simple movement of flexion and inward rotation of the arm and forearm; and this necessarily brought the hand near the point irritated. It is evident that the connection of the sensitive nerve fibres with motor fibres, through the gray matter of the cord, may be such as to call into action muscles which are adapted to accomplish a particular movement, without the intervention of any perception or voluntary impulse. This is the character of the reflex action of the spinal cord.

As a general rule, movements of flexion are adapted to protect the part from external irritation or injury, and are excited by ordinary or moderate causes; those of extension are calculated to repel the foreign substance or to escape from it by moving the whole body, and are only called out by an unusual or excessive stimulus. The defensive or protective character of these movements is often to be seen, in a state of health, when the brain takes no part in their production. If the surface of the skin, for example, be unexpectedly brought in contact with a heated body, the injured part is often withdrawn by a rapid and convulsive movement, before we feel the pain, or even fairly understand the cause of the involuntary act. When the body by any accident suddenly loses its balance, the limbs are thrown into a flexed position, calculated to protect the exposed parts and to break the fall, by a similar involuntary and instantaneous movement. Notwithstanding, therefore, the evident utility of these actions, they have no intentional character, and there is not even any distinct consciousness of their object.

The spinal cord has also an important action in regard to the *attitude* and to *locomotion*. The preservation of the attitude alone requires the harmonious action of many different muscles, all of which contribute in various degrees to the position of the whole body. This is especially the case in man, where, in the standing posture, the body is balanced upon its narrow supports, in such a way as to preserve its equilibrium without attention or fatigue. In the movements of locomotion also, the different flexors and extensors of the anterior and posterior limbs are associated in a manner peculiar to each species of animal; and in man the balancing of the body requires, in progression, a still more extensive combination of muscular action than when at rest.

The spinal cord by itself is not sufficient to produce the muscular actions required for standing and locomotion; since we know that any sudden lesion which deeply injures the brain, or cuts off the medulla oblongata, or divides the spinal cord above the cervical or lumbar enlargements, either in mammalia or in man, instantly destroys the power of standing upright, or of making any effective movements of locomotion. In the frog, an attitude very similar to the natural one is often preserved after decapitation, since the body rests by most of its under surface upon the ground; and the contact of the integument, through the reflex action of the spinal cord, brings the limbs underneath it in a flexed position. If such a frog be held suspended in the air, the limbs hang down in a relaxed condition, and again assume the natural attitude of flexion, when replaced in contact with a hard surface; and, according to Poincaré,[1] it can sometimes be made to execute a series of leaps, each concussion, as the body strikes the ground, giving a fresh stimulus for another reflex movement of extension in the limbs. But in the case of the frog and of the amphibious reptiles generally, the muscular actions required, both for the attitude and for locomotion, are of the simplest character. In the warm-blooded quadrupeds and in man, on the other hand, the act of volition is essential for either standing or progression; and both these powers are abolished by cutting off the communication of the spinal cord with the brain.

But, although the voluntary impulse is necessary to produce the acts of standing or walking, it does not seem to be concerned in the details of their mechanism. Once excited, the nervous action by which walking is accomplished may be kept up without any mental effort, the attention being directed to something else. All we have to do is, to commence the process by an act of volition, and the requisite nervous machinery is at once set in motion. If we decide to turn a corner, all the muscular combinations necessary for that purpose are effected without the immediate intervention of the consciousness or the will. This secondary action, by which the different motor impulses are combined in the limbs and trunk, is undoubtedly dependent upon the integrity of the spinal cord.

The precise mode in which this action is accomplished is not positively ascertained. The most probable explanation at present known is that it is due to a constant reflex activity of the cord, by which the muscles in different parts of the body and limbs are kept in the proper degree of tension or relaxation; and that the different parts of the cord are united with each other for this purpose by longitudinal commissural fibres which enter and leave its gray substance at successive points. Some authors (Todd, Vulpian, Poincaré) adopt the opinion that the *posterior columns* constitute such longitudinal commissures. The reasons for this opinion are not fully satisfactory, since anatomical investigation has thus far failed to show what is the actual origin and

[1] Leçons sur la Physiologie du Système Nerveux. Paris, 1873, p. 72.

termination of the longitudinal fibres of these columns; but there are several facts which give it a strong degree of probability. The three principal reasons in support of this view are as follows:

I. The posterior columns, as fully shown by direct experiment, are not the necessary organs of transmission for either sensation or voluntary motion; and they are, nevertheless, composed of nerve fibres which run in a longitudinal direction. In all the white columns of the cord, in their deeper parts, where they lie in contact with the gray substance, there are oblique or horizontal fibres, entering or emerging from the gray substance, which may either belong to the anterior and posterior nerve roots, or may be commissural fibres running lengthwise from one part of the cord to the other.

II. According to Vulpian,[1] if the posterior columns be divided by several transverse sections, at intervals of two or three centimetres distance from each other, the effect of the operation is a singular disturbance in the power of locomotion, like what would be produced by a loss of harmony in muscular action.

III. The most important facts, however, bearing on this question, are those connected with the disease in man, known as *locomotor ataxia.* In this affection there is a remarkable difficulty in walking, of such a character that the patient's natural gait is altered, and he is no longer sure of his movements. He loses more or less the power of equilibrium, and cannot guide his foot to a particular point without looking at it and at the same time making a direct effort of the will. Consequently locomotion, as it is usually performed, becomes impossible; and yet the patient has not lost the power of voluntary movement in any degree, since he can often exert as much muscular force as ever in grasping an object or in simply pushing or pulling with his legs or arms. But he has lost the power of guiding his movements by an involuntary combination, so as to perform with ease the act of ordinary locomotion. It is for this reason that the affection is called "ataxia," and not paralysis.

In this disease the only parts of the nervous system which are always found to be affected are the posterior columns of the spinal cord. They are the seat of a structural degeneration termed "sclerosis," in which the elements of the connective tissue are increased in quantity and density, while the nerve fibres are altered and atrophied, or finally disappear altogether. According to Brown-Séquard, an alteration limited to a small extent of the posterior columns does not usually affect the voluntary movements; but if it extend for a few inches in length, in either the cervical or the dorso-lumbar region, it always causes a disturbance of these movements; and when it occupies the whole length and thickness of these columns, the patient can neither stand nor walk, although while lying down and with the aid of vision he can move his limbs freely in any direction.

[1] Leçons sur la Physiologie du Système Nerveux. Paris, 1866, p. 381.

Another important action of the spinal cord, as a nervous centre, consists in its control over the *sphincters* and the *organs of evacuation*.

While the small intestine, the cæcum, and the colon are supplied exclusively with nerves from the abdominal plexuses of the sympathetic system, the lower portion of the rectum receives branches from the sacral plexus of spinal nerves, which are distributed both to its mucous membrane and its muscular apparatus. The lower part of the large intestine acts in great measure as a temporary reservoir, in which the feces, brought down from above by peristaltic movement, accumulate until the time arrives for their evacuation. The rectum, in man, is usually empty, or nearly so, until shortly before evacuation; and when the feces begin to pass into it from above, it is still capable of retaining them for a certain period. Their retention and discharge are provided for, in this part of the alimentary canal, by two sets of muscular fibres; namely, first, the sphincter ani, which keeps the orifice of the anus closed; and secondly, the levator ani and the circular fibres of the rectum itself, which by their contraction open the anus and expel the feces. Both these acts are regulated by the reflex influence of the spinal cord.

In the natural condition, the sphincter ani is habitually in a state of contraction, thus preventing the escape of the contents of the intestine. Any external irritation, applied to the verge of the anus, causes increased contraction of its fibres and a more complete occlusion of its orifice. This habitual closure of the sphincter is an entirely involuntary act, as efficient during profound sleep as in the waking condition, and depends upon the reflex action of the spinal cord.

But when the rectum is distended to a certain point by feces passing into it from above, the nervous action changes. The impression then produced upon the mucous membrane of the rectum, conveyed inward by its sensitive nerve fibres to the spinal cord, causes a relaxation of the sphincter ani. At the same time the levator ani draws the borders of the relaxed orifice upward and outward, and the feces are expelled by the contraction of the muscular fibres of the rectum itself.

Both these actions are in some degree associated, in a state of health, with sensation and volition. The distension of the rectum which precedes an evacuation is usually accompanied by a distinct sensation, and the resistance of the sphincter may be intentionally prolonged for a certain period. But this voluntary power over the muscular contractions is limited. After a time the involuntary impulse, growing more urgent with the increased distension of the rectum, becomes irresistible; and the discharge finally takes place by simple reflex action of the spinal cord.

If the irritability of the cord be exaggerated by disease, while its connection with the brain remains entire, the distension of the rectum is announced by the usual sensation; but the reflex impulse to evacuation is so urgent that it cannot be controlled by the will, and the patient

is compelled to allow it to take place at once. The discharges are then said to be "involuntary."

If the cord, on the other hand, be injured or divided in its middle or upper portions, the sensibility and voluntary action of the sphincter are lost, because its connection with the brain has been destroyed. The evacuation then takes place at once, by the ordinary mechanism, as soon as the rectum is filled, but without any knowledge on the part of the patient. The discharges are then said to be "involuntary and unconscious."

Finally, if the lower portion of the cord, in the living animal, be broken up by means of an instrument introduced into the spinal canal, the tonic contraction of the sphincter ani at once disappears. The same effect is produced, in man, by disorganization of the lower part of the spinal cord from injury or disease. The sphincter ani is then permanently relaxed, and the feces are evacuated almost continuously, without the knowledge or control of the patient, as fast as they descend into the rectum from the upper portions of the intestinal canal.

The *urinary bladder* is also an organ both of reservoir and evacuation, which is protected by the circular bundle of muscular fibres at the commencement of the urethra, known as the "sphincter vesicæ." While the nerves distributed to the kidneys are derived exclusively from the cœliac plexus of the sympathetic system, those of the bladder consist partly of sympathetic filaments from the mesenteric ganglia, and partly of cerebro-spinal filaments from the lumbar portion of the spinal cord, both of these sets having united in the abdomen to form the hypogastric plexus.

The tonic contraction of the vesical sphincter during health, by which the urine is retained in the bladder, is a continuous, involuntary, and unconscious act, like that of the sphincter ani. When the time comes for evacuation, the sphincter is relaxed by a voluntary impulse, and the muscular coat of the bladder contracts so as to expel its contents; but although the commencement of this process is a voluntary one, the subsequent contraction of the muscular walls of the bladder continues without any effort of the will. According to the experiments of Giannuzzi[1] on dogs, irritation of the lumbar portion of the spinal cord by pricking with a steel needle, causes contraction of the urinary bladder; and these contractions are no longer produced after division of the roots of the sacral nerves. Irritation of either the sympathetic or the spinal nerve filaments going to the hypogastric plexus produced contraction of the bladder, but these contractions were more energetic in the latter case than in the former.

Diseases or injuries of the spinal cord which cause complete paraplegia, also usually produce a paralysis of the bladder. So far as regards contraction of the bladder itself, therefore, this act is under the influence both of the sympathetic and cerebro-spinal systems; but its

[1] Journal de la Physiologie. Paris, 1863, tome vi. p. 22.

most energetic stimulus is derived from the spinal cord through the sacral nerves.

The closure or relaxation of the sphincter vesicæ, on the other hand, is regulated by nervous influences coming from the cerebro-spinal system alone. The contraction of the sphincter offers a resistance to the escape of fluid from the bladder, which may be measured, and which was found by Kupressow,[1] in the rabbit, to be equal to the pressure of a column of water more than 40 centimetres in height. That is, if in the living animal one of the ureters were closed by a ligature, and an upright tube fastened in the other, the bladder and the upright tube might be filled with water to a height, on the average, of 44 centimetres without any of it escaping by the urethra; beyond that point the contractile power of the sphincter was overcome, and the water was discharged by the urethral orifice.

The experiments of Kupressow also show that the nervous centre upon which the sphincter vesicæ depends for its reflex stimulus is in the lumbar portion of the spinal cord. For if the cord were divided at the level of the first or second lumbar vertebræ, no difference was perceptible in the amount of resistance to pressure offered by the sphincter; and sections at the levels of the third and fourth lumbar vertebræ made a difference of only two centimetres. But if the section of the cord were made at the fifth lumbar vertebra, the resistance of the sphincter was at once reduced to 14 centimetres; and the same effect was produced by section at the sixth and seventh vertebræ of the same region. The tonic contraction, therefore, of the sphincter vesicæ, although it may be aided by an act of volition, is directly dependent upon a nervous centre situated, in the rabbit, about the middle of the lumbar portion of the spinal cord; since this contraction persists after the cord has been separated from the brain by a section at or above the fourth lumbar vertebra, while it disappears if the section be made at or below the fifth lumbar vertebra, thus either destroying the nervous centre itself or cutting off its communication with the bladder.

Both the retention of the urine in the bladder and its evacuation may also be accomplished without the aid of any voluntary act. This is shown by the experiments of Goltz,[2] who found that after division of the spinal cord, in dogs, between the dorsal and lumbar regions, the animals, though deprived of sensibility and voluntary motion in the posterior parts of the body, could often retain their urine for a considerable time, and also evacuate it by a regular and forcible contraction of the bladder.

In man, when the sensibility of the mucous membrane of the bladder or neighboring parts is increased by inflammation, the reflex impulse to micturition is increased in intensity, producing an intolerance of urine. Under these circumstances the urine is discharged by a reflex act as

[1] Archiv für die gesammte Physiologie. Bonn, 1872, Band v. p. 291.

[2] Archiv für die gesammte Physiologie. Bonn, 1874, Band viii. p. 474.

soon as a small quantity of it has accumulated in the bladder. The impression which excites this discharge is accompanied by a conscious sensation, but is too urgent to be resisted by the will.

On the other hand, injury or destruction of the spinal cord in the dorsal region may cut off all sensibility and voluntary power over the bladder, and yet the organ may be evacuated at regular intervals by the reflex action of the lumbar portion of the cord. But in diseases or injuries affecting extensively the lower portion of the cord, a complete paralysis of the bladder is often produced. The patient is consequently unable to discharge his urine in the ordinary way, and requires to be relieved by the introduction of a catheter. If this be not done, the urine accumulates in the bladder; being retained for a time by the elastic tissues surrounding the neck of the bladder and the urethra. But after the distension of its walls has reached a certain point, the mechanical resistance of the bladder becomes too great to allow any further accumulation; and the urine dribbles away from the urethra as fast as it is excreted by the kidneys. Paralysis of the bladder, accordingly, first causes a permanent distension of the organ, which is afterward followed by a continuous, passive and incomplete discharge of its contents.

The spinal cord, therefore, in its character as a nervous centre, exerts a general protective influence over the whole body. It presides over the involuntary movements of the limbs and trunk; it supplies the requisite nervous connection between different muscular actions for the attitude and locomotion; and by its control over the muscular apparatus of the rectum and bladder, it regulates the accumulation and discharge of the excrementitious products of the system.

CHAPTER V.

THE BRAIN.

THE brain, or encephalon, comprises all that portion of the cerebro-spinal axis which is contained within the cavity of the cranium. It consists of a variety of nervous centres, or collections of gray substance, connected with each other and with that of the spinal cord by tracts of longitudinal, transverse, oblique, and radiating nerve fibres. The results of experimental investigation leave no doubt that each one of these different nervous centres has a special function, more or less independent of the others in its immediate action, though necessarily connected with the rest in the production and external manifestation of the nervous phenomena. They are situated upon both sides of the median line, and are, for the most part, evidently arranged in symmetrical pairs, like the hemispheres of the cerebrum, the cerebral ganglia, the olfactory lobes, the tubercula quadrigemina, and the two halves of the cerebellum. The largest of these nervous centres, forming in man nearly four-fifths of the mass of the entire brain, are the two convoluted masses known as the "hemispheres" of the cerebrum.

The Hemispheres.

The hemispheres form two ovoidal masses of nervous matter, flattened against each other at the median line, where they are separated by the great longitudinal fissure, corresponding to the posterior median fissure of the spinal cord, and presenting on their lateral surfaces a general rounded or hemispherical form, whence their name is derived. They consist externally of a layer of gray nervous substance, and internally of a mass of white substance, the fibres of which may be said in general terms to radiate from the cerebral ganglia (corpora striata and optic thalami) toward the cortical layer of the hemispheres. The external layer of gray substance, and consequently the surface of the hemispheres, is thrown into numerous folds or convolutions, which are separated from each other by fissures, generally from 10 to 25 millimetres deep. These fissures, like the great longitudinal fissure in the median line, are simply spaces where the opposite surfaces of two adjacent convolutions lie in contact with each other; and they indicate the points at which the external layer of gray matter dips down toward the interior, to return upon itself and form the next convolution. The larger quantity of gray substance is, therefore, situated at the fissures rather than at the projecting edges of the convolutions between them; and the more

numerous and deeper the fissures upon the surface of a brain, the greater is the amount of gray substance which it contains.

Although the cerebral fissures and convolutions are never all precisely the same in any two brains, nor even exactly symmetrical in the two hemispheres of a single brain, yet the principal ones are sufficiently constant to be regarded as essential features of the organ; and the remainder, while varying within certain limits, exhibit a general arrangement which is characteristic of the species of animal to which they belong. In man they attain a very high degree of development; and their nomenclature is important as enabling us to recognize different parts of the cerebral surface.

Fig. 156.

Plan of the Fissures and Convolutions of the Human Brain.—The fissures are designated by letters, the convolutions by numbers. S. Fissure of Sylvius; *a.* Anterior ascending branch; *b.* Posterior horizontal branch. R. Fissure of Rolando. P. Parietal fissure. 1. First frontal convolution. 2. Second frontal convolution. 3. Third frontal convolution. 4. Anterior central convolution. 5. Posterior central convolution. 6. Supra-Sylvian, or supra-marginal convolution. 7. Superior temporal convolution. 8. Angular convolution. 9. Middle temporal convolution. 10. Inferior temporal convolution. 11. Upper parietal convolution. 12. Occipital convolutions.

Next in importance to the great longitudinal fissure, which separates the two hemispheres upon the median line, is the *Fissure of Sylvius* (S). This is a much deeper cleft than the others, and exists, according to Prof. Wilder, in the brains of all animals where the cerebral surface is fissured at all. In the human fœtus it is the first to appear, being visible as early as the third month; and in the adult it forms a basis for

the whole geographical division of the hemisheres. It commences as a transverse indentation on the under surface of the brain, running thence outward, backward, and upward, thus forming the anterior boundary of the middle or temporal lobe. In the inferior animals, the whole hemisphere is seen to be curved round this fissure, the convolutions generally following its course and bending round its upper extremity in an arched form; and in the human brain this arrangement of the lateral convolutions is also distinctly visible.

On the outer side of the cerebral hemisphere, where it emerges from the base of the brain, the fissure of Sylvius presents, in man, two distinct branches, namely a shorter, anterior, ascending branch (a), and a longer, posterior, more horizontal branch (b, b, b). At its middle and anterior portions, this fissure is very deep, and conceals within its folds a projecting group of short radiating convolutions, belonging to the under surface of the brain, between the anterior and temporal lobes, called the "Island of Reil."

The second fissure in importance, visible upon the convexity of the hemisphere, is the *Fissure of Rolando* (R). This fissure runs from near the median line transversely outward and somewhat obliquely forward, reaching nearly to the middle of the fissure of Sylvius, and forming the boundary line between the frontal and parietal portions of the hemisphere. It is bordered by two convolutions, one on each side, running parallel with itself, namely, the anterior and posterior central convolutions (4, 5).

The third principal fissure is the *Parietal Fissure* (P). It starts from immediately behind the posterior central convolution, and runs backward through the parietal portion of the hemisphere, curving somewhat downward upon itself toward its posterior extremity. Outside and below it are the arched convolutions about the fissure of Sylvius; inside and above it is a convolution running parallel with the great longitudinal fissure.

Beside the three fissures just named there are five others, which, though less deep and strongly marked, are constantly present and show a considerable regularity in their position and arrangement. Three of them are in the anterior or frontal lobe, in front of the fissure of Rolando. The first runs parallel with the fissure of Rolando, and a little in advance of it, toward the anterior extremity of the hemisphere. It is called the "præcentral fissure." The second runs through nearly the whole length of the frontal lobe, in a general direction parallel with that of the great longitudinal fissure. It divides the upper from the middle portion of the frontal lobe, and is called the "superior frontal fissure." The third is the "inferior frontal fissure," and surrounds the upper end of the short ascending branch of the fissure of Sylvius. The two remaining fissures of this grade, visible in a lateral view of the brain, are situated in the temporal lobe, below and behind the fissure of Sylvius, with which they run in a general parallel direction.

In addition to the fissures already described there are many others

of secondary importance and more irregular in location, which increase the convoluted aspect of the cerebral surface. Some of them run longitudinally along the middle of a convolution, dividing it into two narrower parallel folds; and some of them pass transversely from one of the main fissures to another, appearing to cut across the intervening convolution. But in many instances, if the arachnoid and pia mater be removed, it will be found that these secondary fissures are merely superficial indentations on the surface, or furrows for the accommodation of a vascular branch; and that they do not, like the others, penetrate deeply into the substance of the brain.

The principal convolutions to be distinguished on the convexities of the hemispheres are as follows:

The *First Frontal Convolution* (1) runs from the upper end of the anterior central convolution, just in front of the commencement of the fissure of Rolando, forward along the edge of the great longitudinal fissure to the anterior extremity of the frontal lobe, where it bends downward and backward, terminating below in a straight convolution next the median line, and resting upon the upper surface of the orbital plate. This convolution is divided and folded in many ways by secondary transverse, oblique, and longitudinal fissures, but its general direction is easily recognized. It is bounded externally by the superior frontal fissure.

The *Second Frontal Convolution* (2) also takes its origin at the anterior central convolution, from which it is more or less completely separated by the præcentral fissure; thence running downward and forward over the anterior and lateral part of the frontal lobe. This is the widest of the three frontal convolutions, and the most abundantly variegated by secondary folds and fissures. It is separated from the first frontal convolution by the superior frontal fissure, and from the third by the inferior frontal fissure.

The *Third Frontal Convolution* (3) is situated at the lower and outer part of the frontal lobe, and curves round the anterior ascending branch of the fissure of Sylvius. It communicates posteriorly with the lower end of the anterior central convolution, and by this portion of its substance helps to cover in and conceal the island of Reil at the bottom of the fissure of Sylvius.

The *Anterior Central Convolution* (4) runs transversely outward and forward along the front edge of the fissure of Rolando. It is usually a single convolution, but is more or less folded laterally by transverse indentations. It communicates with the first frontal convolution above and with the third frontal convolution below. It also curves round the lower end of the fissure of Rolando, to unite with the following convolution, which may be said to be a continuation of it.

The *Posterior Central Convolution* (5) also runs parallel with the fissure of Rolando, but behind it. Above, it turns backward and is continuous with the convolutions of the upper part of the parietal lobe.

The *Supra-Sylvian or Supra-marginal Convolution* (6) starts from the lower end of the posterior central convolution and thence arches round the extremity of the fissure of Sylvius. It then continues its curvilinear course, running downward and forward, parallel with the inferior margin of the fissure of Sylvius, toward the anterior extremity of the temporal lobe. In this situation it is known as the *First Temporal Convolution* (7). Throughout its course, it is generally divided into two parallel convolutions by a secondary fissure running along its axis, and both of these secondary convolutions are more or less folded transversely.

The *Angular Convolution* (8) originates from the preceding and follows the inferior edge of the parietal fissure backward to its posterior extremity, where it makes a rather sharp turn downward and forward, whence its name of the "angular convolution." It then becomes continuous with the *Second Temporal Convolution* (9) running downward and forward to the extremity of the temporal lobe. Below this portion, and running parallel with it, is the *Third Temporal Convolution* (10) which forms the inferior border of the temporal lobe.

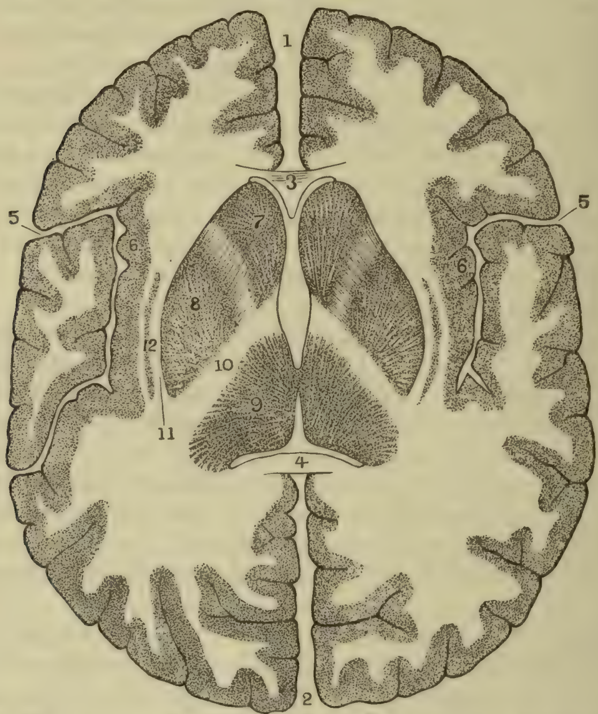
The *Upper Parietal Convolution* (11) is situated above the parietal fissure, between it and the posterior part of the great longitudinal fissure. Like the corresponding frontal convolutions, it is much divided by irregular secondary foldings, and is connected with other convolutions which are concealed within the great longitudinal fissure. There are also a number of *Occipital Convolutions* (12), both longitudinal and transverse, but these are not conspicuous in a lateral view of the cerebral hemispheres. They are more or less continuous with the upper parietal convolution above, and with the second and third temporal convolutions below.

On a transverse horizontal section of the brain, the convolutions are seen to penetrate into its substance for varying distances at different regions. In the anterior and posterior parts the foldings are more nearly regular in depth, and leave a comparatively thick layer of white substance between the cerebral ganglia and the gray matter of the convolutions. But at the sides of the brain, at the situation of the fissures of Sylvius, the convolutions reach to a much greater depth. The cerebral ganglia are placed on each side the median line, near the centre of the brain; the corpora striata being separated from each other anteriorly by the septum lucidum and the cavity of the lateral ventricles, and the two optic thalami being separated in a similar manner by the cavity of the third ventricle, except where they are united by the soft commissure.

The optic thalami (Fig. 157, $_9$) are surrounded on their outer borders, and separated from the corpora striata, by a band of white substance, the *internal capsule* ($_{10}$) consisting of fibres passing upward from the crura cerebri. The corpora striata ($_{7,8}$) form on each side, at their inferior portions, a continuous mass of gray substance; but for the greater part of their thickness they are divided into two parts by a tract of white substance, continuous with the internal capsule, and, like it, con-

sisting of bundles of ascending fibres derived from the crura cerebri. The anterior and more internal of the two parts into which the corpus striatum is thus divided is the *caudate nucleus* ($_7$), so called because a horizontal section through its uppermost portion exhibits a slender,

Fig. 157.



HORIZONTAL SECTION OF THE HUMAN BRAIN, at the level of the cerebral ganglia. —1, 2. Anterior and posterior portions of the great longitudinal fissure. 3, 4. Anterior and posterior parts of the corpus callosum. 5. Fissure of Sylvius. 6. Beginning of the convolutions of the Island of Reil. 7, 8. Corpus striatum. 7. Caudate nucleus. 8. Lenticular nucleus. 9. Optic thalamus. 10. Internal capsule. 11. External capsule. 12. Claustrum.

tail-like prolongation in a backward direction; the posterior and more lateral part is called the *lenticular nucleus* ($_8$), from its having, in a section at its mid-level, a tolerably regular lens-like figure. Both the optic thalamus and the corpus striatum are traversed by slender bundles of fibres, visible to the naked eye, and which have a generally radiating direction upward and outward.

The outer surface of the lenticular nucleus is inclosed by a thin layer of white substance, the *external capsule* ($_{11}$), in which is also to be seen a very narrow band of isolated gray substance, termed the "claustrum" ($_{12}$). At this situation the layer of gray substance at the bottom of the fissure of Sylvius is separated from the corpora striata by only a very narrow interval; and the fibres running outward and downward

from these bodies would reach almost immediately the convolutions of the Island of Reil.

Intimate Structure of the Hemispheres.—As the longitudinal tracts of white substance pass upward and forward from the medulla oblongata and tuber annulare to the base of the hemispheres, they form the two irregularly cylindrical masses known as the "crura cerebri." Their fibres plunge, for the most part, directly into the substance of the corpora striata in front, and of the optic thalami behind; while from these two pairs of ganglia other fibres emerge into the white substance of the hemispheres. A portion of the fibres, however, coming from the crura cerebri, pass, according to Vulpian, Henle, and Meynert, uninterruptedly onward, in the internal capsule between the optic thalamus and corpus striatum, and between the two nuclei of the corpus striatum; thus reaching the white substance of the hemispheres without having traversed the gray matter of the ganglia.

From this level, that is, above and outside of the cerebral ganglia, the ascending divergent tracts of white substance form a spreading crown of nerve fibres, which radiate in all directions to the layer of gray substance on the exterior. These fibres are of very small size, as compared with those in the peripheral portion of the nervous system; their average diameter, according to Kölliker, being 4.5, and none of them being larger than 6.7 micro-millimetres in thickness.

The general direction of the radiating nerve fibres is easily seen, in brains hardened in alcohol, to be that described above. At the same time, microscopic examination shows that they are abundantly mingled with other fibres which cross them at right angles, or nearly so, and which are to be found more or less in every portion of the white substance of the hemispheres. These horizontal or curvilinear cross fibres are derived in great measure from the lateral expansions of the *corpus callosum*, the transverse fibres of which spread out in various directions, bending toward the convolutions of the upper, middle, and lower part of the hemispheres. As these fibres come from the median line at the level of the corpus callosum, they necessarily cross those which are ascending from the cerebral ganglia below. The corpus callosum is consequently a great transverse commissure, uniting the two hemispheres of the cerebrum with each other. There are also fibres immediately beneath the cortical layer of gray substance, following the curve of the convolutions where they project inward into the white substance. These are known as the "arciform fibres," and are regarded as connecting filaments between the gray substance of adjacent convolutions.

The *gray substance* of the cerebral convolutions forms an external layer, from two to three millimetres in thickness, into which the fibres of the white substance penetrate from within in a perpendicular manner. It consists of a uniform granular matrix, in which are imbedded the nerve cells, and through which the fibres continue their course in various directions. The nerve cells are rounded or irregular in form, with a varying number of simple or branched prolongations. In the middle

Fig. 158.

Vertical Section of one of the Cerebral Convolutions; showing pyramidal cells, and bundles of fibres passing outward from the white substance. Magnified 300 diameters. (Henle.)

portion of the layer of gray substance, the cells are distinguished by their pyramidal form; the pointed extremity of the cell being, with few exceptions, directed toward the surface of the brain, and the base toward the white substance of the interior. According to Henle, they have an average diameter of 15 mmm. Two, three, or sometimes even four prolongations extend from the angles at the base of the cell, running inward toward the white substance, and becoming more or less divided and ramified; while the pointed extremity, on the other hand, extends outward in a single prolongation toward the cerebral surface.

The fibres, as they penetrate from the white into the gray substance, are arranged in bundles, where they at first run in a general direction parallel with each other. But these bundles rapidly diminish in size, as the fibres diverge laterally to pursue a more or less horizontal course; and in the external portions of the gray substance there are only isolated fibres running in various directions. In the gray substance, the nerve fibres become reduced to their smallest dimensions, measuring, according to Kölliker, from about 1 to 2 mmm. in diameter. Some of them spread out at various levels in the cortical layer, while others continue a vertical or oblique course quite to the superficial portions of the gray substance.

The immediate relation between the fibres and cells of the gray substance of the hemispheres has not been determined

with absolute certainty. Although a few isolated instances have been reported in which a cell prolongation has been seen to become continuous with a medullated nerve fibre, it is usually impossible to demonstrate this by direct observation, and some of the best microscopists have been unable to see it in a single instance. The probability that such a connection exists is assumed from the fact that many of the nerve fibres in the gray substance become so slender and pale as to resemble very closely the cell prolongations; and, on the other hand, the cell prolongations frequently run in the same direction with the nerve fibres. According to Henle[1] the prolongations, given off from the bases of the pyramidal cells, are so often seen to lose themselves in the bundles of nerve fibres coming from the white substance as to justify the assumption that the fibres in these instances terminate in the cells. The delicacy of texture of the gray substance and the distance through which a cell prolongation runs before it attains the character of a nerve fibre may be sufficient reason why the connection is not more frequently seen in microscopic preparations.

Physiological Properties of the Hemispheres.—The importance of the hemispheres, in connection with the higher manifestations of nervous action, is sufficiently indicated by their excessive development in man, as compared with the other portions of the encephalon. For while in the lower mammalians they are of medium size, and often smooth or sparingly convoluted upon their surface, and in reptiles and fish are sometimes hardly larger than the other nervous centres of the brain, in man they acquire such an extension as to cover and surround almost completely every other part of the encephalic mass, their superficial layer of gray substance being at the same time still further increased by the multiplied convolutions of its surface.

Notwithstanding, however, the evident importance of the hemispheres as special parts of the nervous system, the first fact certainly known in regard to them is that *they are not*, *even in man*, *directly essential to life.* That is to say, they do not hold under their immediate control any of the physiological acts, like those of respiration and circulation, which are necessary to the continuance of vitality. They often influence these acts, in an indirect manner, by the sympathetic connections of the nervous system; but life will continue for a certain period under the influence of other nervous centres, without the aid of the cerebral hemispheres.

This is readily demonstrated in some of the lower animals by the entire removal of the hemispheres on both sides. In man, extensive morbid changes may take place in these parts, or severe mechanical injuries, accompanied by greater or less loss of substance, may be inflicted upon them without producing a fatal result. In a case reported by Prof. Detmold,[2] of abscess in the anterior lobe of the brain, a knife

[1] Anatomie des Menschen. Braunschweig, 1871, Nervenlehre, p. 270.

[2] American Journal of the Medical Sciences. Philadelphia, January, 1850.

was passed into the cerebral substance, making a wound one inch in length and half an inch in depth, when the abscess was reached and pus discharged. The patient immediately aroused from his comatose condition, and was able to speak; but the collection of pus afterward returned, and the patient finally died at the end of seven weeks from the time of opening the abscess.

In another case,[1] a pointed iron bar, three feet and a half in length, and one inch and a quarter in diameter, was driven through a man's head by the premature blasting of a rock. The bar entered the left side of the face, near the angle of the jaw, and passed obliquely upward, inside the zygomatic arch and through the anterior part of the cranial cavity, emerging from the frontal bone at the median line, just in front of the point of union of the coronal and sagittal sutures. The patient became delirious within two days after the accident, and subsequently remained partly delirious and partly comatose for about three weeks. He then began to improve, and at the end of rather more than two months from the date of the injury was able to walk about. At the end of sixteen months the wounds were healed, and the patient had recovered his general health, though with loss of sight in the eye of the injured side.

The patient survived for a little over twelve years, being able to do the ordinary work of an ostler, coachman, and farm-laborer, in all of which occupations he was employed at various intervals. He died in 1861, after a short illness accompanied by convulsions. The skull, which was subsequently deposited in the Warren Anatomical Museum,[2] shows the openings corresponding with the points of entrance and exit of the iron bar.

The conclusions derived from comparative anatomy, from pathological observations in man, and from experiments upon animals, all show that the cerebral hemispheres are especially connected with the manifestations of *conscious intelligence*, as distinguished from involuntary reflex actions, simple sensations, or instinctive movements.

I. So far as we can judge of the character and extent of these manifestations in the lower animals, they correspond directly with the development of the hemispheres, rather than with that of any other portion of the encephalon. In many of the lower animals, muscular power and endurance, the activity of some of the special senses, and the promptitude and certainty of the instincts, are much greater than in man; while in the human species, the intelligence is the only faculty which is invariably superior to that of animals, and which always gives to man the advantage over them. Even among animals, that which especially characterizes certain species, and which most nearly resembles that of man, is a *teachable* intelligence; that is, one which understands the meaning

[1] American Journal of the Medical Sciences, Philadelphia, July, 1850.

[2] J. B. S. Jackson, Descriptive Catalogue of the Warren Anatomical Museum. Boston, 1870, p. 145.

of impressions or objects presented to it, and thus enables its possessor, by comprehending and retaining new ideas, to profit by experience.

II. The general result of injury, disease, or disorganization of the hemispheres in man, especially affecting the gray substance of the convolutions, is a disturbance, diminution, or suspension of the intellectual faculties. In these cases, among the earliest and most constant of the morbid phenomena is a loss or impairment of memory. The patient forgets the names of particular objects or of particular persons; or he is unable to calculate numbers with his usual facility. His mental derangement is often shown in the undue estimate which he forms of passing events. He is no longer able to appreciate the relation between different objects and phenomena. He will show an exaggerated degree of solicitude about a trivial occurrence, and will pay no attention to matters of real importance. As the difficulty increases, he becomes careless of directions and advice, and must be managed like a child or an imbecile. Finally, when the injury to the hemispheres is complete, the senses may still remain active and impressible, while the patient is completely deprived of intelligence, memory, and judgment. The constancy of these results when the lesion is situated in the hemispheres, and the fact that they often occur without being accompanied by any loss of sensibility or motion, show the close connection between the mental powers and the nervous action of this portion of the brain.

The same connection is seen in the existence of congenital idiocy with imperfect development of the brain. In many cases the immediate condition upon which the idiocy depends is the small size of the brain as a whole, particularly conspicuous in the cerebral hemispheres. The general and special senses, and the activity of the nervous system at large, are sometimes fully developed in these instances, while the intelligence proper remains at so low a grade, that no improvement in the mental operations is possible and teaching is almost without effect.

This was the case, in a marked degree, with a pair of dwarfed and idiotic Central American children, who were exhibited at one time in the United States, under the name of the "Aztecs." They were a boy and a girl, aged respectively about seven and five years.

The antero-posterior diameter of the boy's head was only $4\frac{1}{2}$ inches, the transverse diameter less than 4 inches. The antero-posterior diameter of the girl's head was $4\frac{1}{3}$ inches, the transverse diameter only $3\frac{3}{4}$ inches. The habits of both, so far as regards feeding and taking care of themselves, were those of children two or three years of age. They were incapable of learning to talk, and could only repeat a few isolated words. Notwithstanding, however, their limited intelligence, they were remarkably vivacious and excitable. While awake they were in almost constant motion, and any new object or toy presented to them immediately awakened a lively curiosity. They understood readily the meaning of those who addressed them, so far as it could be conveyed by gesticulation and the tone of voice; but they could not be made to comprehend

Fig. 159.

THE "AZTEC" IDIOTIC CHILDREN.—Taken from life, at five and seven years of age.

articulate language, and, as in other idiots, mental instruction was without result.

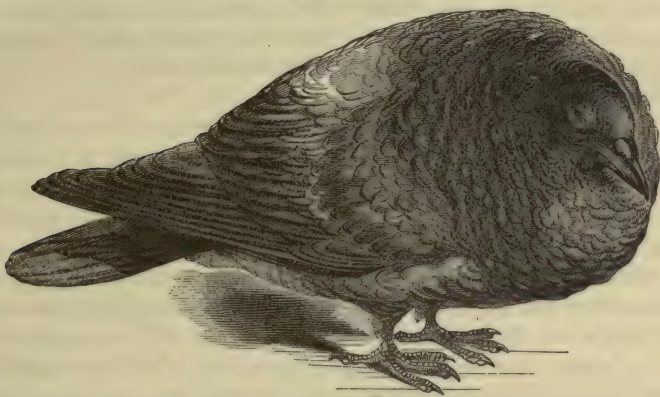
III. Experiments performed upon the lower animals, by removal of the hemispheres, lead to a similar result. In large and full grown mammalians the injury is usually fatal, owing in great measure to the attendant hemorrhage; but it may be performed in fish, reptiles, birds, and sometimes in young quadrupeds without producing death. Vulpian has succeeded in maintaining life, after this operation, in the frog, the turtle, the pigeon, the cock, the rabbit, and the rat. The result is that these animals retain their sensibility and power of motion, and continue to maintain the normal attitude and to perform many instinctive and reflex movements; but spontaneous action, and its conscious adaptation to external conditions, is abolished with the removal of the cerebral hemispheres.

The operation is very readily performed upon the pigeon, and its effects in this animal are uniform and distinctly marked. After removal of both hemispheres, the bird maintains without difficulty the standing posture, and will even rest upon a perch with security if undisturbed; but he remains in a state of profound quietude, almost completely indifferent to surrounding objects. He stands upon the ground or rests upon his perch, with the eyes closed and the head sunk between the shoulders. The plumage is smooth and glossy, but is uniformly expanded, by erection of the feathers, so that the body appears puffed out and larger than natural. Occasionally the bird opens his eyes, stretches his neck, shakes his bill once or twice, or smooths down the feathers upon his shoulders, and then relapses into his former apathetic condition. This characteristic state of immobility comes on immediately after removal of the hemispheres.

It is not accompanied, however, by loss of either general or special sensibility. If the foot of the bird be pinched with a pair of forceps, he becomes partially roused and moves uneasily once or twice from side to side, as if to escape the irritation. Vulpian has seen a pigeon within a

short time after the operation shake the head briskly in consequence of a fly having alighted on the wound. Hearing and sight also remain. The discharge of a pistol behind the back of the pigeon will often cause him to open his eyes and turn his head partially round, giving evident signs of having heard the report; though he immediately becomes quiet again and pays it no further attention. In a rat which had been subjected to this operation by Vulpian, a sharp hissing sound made by the lips produced a sudden start and movement of the whole body. The same observer found that in a pigeon, after the animal had been roused

Fig. 160.



PIGEON, AFTER REMOVAL OF THE CEREBRAL HEMISPHERES.

by pinching the foot, the sudden approach of a hand toward the eye caused a winking movement with partial turning of the head. Sometimes such a pigeon will fix his eye on a particular object, and watch it for several seconds together. Longet found that by moving a lighted candle before the animal's eyes in a dark place, the head of the bird would often follow the movements of the candle, showing that the impression of light was perceived.

The animal is still capable, therefore, after removal of the hemispheres, of receiving sensations from external objects. But these sensations make upon him no lasting impression. He is incapable of connecting with his perceptions any distinct succession of ideas. If he hears the report of a pistol, he is not alarmed by it; for the sound, though distinctly enough perceived, does not suggest any idea of danger or injury. There is accordingly no power of perceiving the relation between external objects. The memory, particularly, is destroyed, and the recollection of sensations is not retained from one moment to another. The muscles are still under the control of the will; but the will itself is inactive, because it lacks its usual stimulus and direction. The powers which have been lost, therefore, are those of a mental character; that is, the power of comparing different sensations or ideas, of perceiving the

proper relation between them, and of originating in consequence an intelligent volitional act.

The cerebral hemispheres as a whole are therefore evidently the centres in which the nervous mechanism of mental action is accomplished. The mental endowments which are concerned in the manifestations of the intelligence are mainly the memory, the reason and the judgment.

Memory is the simplest and most essential of these faculties for the due performance of intelligent acts. The recollection of names, and of the objects to which they belong, is indispensable even to the use of articulate language; and a deficiency of memory seems often to be the immediate condition upon which the incapacity of idiotic children to talk depends. It is also constantly essential in the ordinary occupations of life, in enabling us to retain past impressions as a guide for immediate or future acts.

The *reason* may be considered as the faculty by which we appreciate the character of the nervous impressions received, and are enabled to refer them to their external source. This is quite different from the simple power of perception, which continues, as experiment has demonstrated, after the removal of the cerebral hemispheres. The mental action which is excited by an impression coming from without is one which transfers the attention from the internal sensation to its external source; and when this action is prompt and effectual, we at once acquire an idea of whence the impression originated and what is its significance. The perfection of this quality consists in the certainty with which it appreciates the relation between an effect and its cause, and the relative importance of different phenomena. This capacity is deficient or absent in idiots, and consequently they cannot avoid dangers or provide for their necessities. For the same reason it is useless to punish an idiot, because, although he may feel the pain inflicted, he does not refer it as a consequence to any previous action of his own. A deficiency of the same quality in the insane, or in those in whom it is naturally imperfect, produces a want of power to comprehend the importance and connection of different events. They are said to be "unreasonable," because they expect results which are unlikely to follow from certain causes, and because they assume the existence of causes which are not really indicated by the results.

The *judgment* is the faculty by which the appropriate means are selected for the accomplishment of a particular end. Its exercise requires the existence of reason and memory, which supply the necessary conditions upon which it is based; but its own action is one which looks to the future rather than to the past. An individual in whom the judgment is well developed employs, under the guidance of experience, means which are well adapted to attain the end he has in view; one who is deficient in this respect resorts to means which are insufficient or inappropriate, and is consequently unsuccessful. Whether the act performed in this manner be a simple mechanical operation, like that of

shutting a door to exclude the cold, or a complicated plan involving many parts, the mental process is the same in kind, and differs only in degree; its essential character being that it is an intelligent act, based upon an understanding of the previous conditions, and intended to accomplish a definite result.

It is evident that all such manifestations of intelligence, taking place through the cerebrum, are reflex actions. Their starting point is a sensation coming from without, which gives rise in the mind to a succession of internal operations, terminating in an intelligent volitional impulse. This is reflected from within outward, and thus finally calls into action the nerves of voluntary motion. There can be little doubt that the intermediate process, between the sensation and the volitional impulse, takes place in the gray substance of the cerebral convolutions.

Special Seat of the Faculty of Articulate and Written Language.—Most of the lower animals have the power of communicating with each other by certain movements and vocal sounds in such a way as to attract their attention, and enable them to act in concert. The language thus employed is always a language of expression, and consists in such modifications of the tone of voice or the position of the limbs as indicate pleasure or dislike, excitement or alarm, or a friendly or hostile disposition. In man the same methods are largely used to express similar feelings, and to represent others, such as surprise, contempt, amusement, or doubt, which do not seem to exist in animals to an appreciable degree.

But man has also the faculty of conveying definite information by means of articulate speech, in which arbitrary sounds are used to indicate special objects, qualities, or acts, as well as all the relations which may exist between them. The power of using articulate language, as a vehicle for the expression of the thoughts, is generally in proportion to the development of the intelligence as a whole. In order that it may be exercised, two faculties must come into action; namely, first, the memory, by which the particular words required are brought to the mind; and, secondly, the voluntary combination of motor impulses necessary for their articulation. These acts are performed, in health, with such rapidity that we are not conscious of them; and the exercise of speech seems to be a direct consequence of the ideas which are to be expressed. But pathological cases show that either one or both of these faculties may be absent, while the ideas and the desire to express them are as distinct as ever.

The affection, in these cases of loss of the power of language, is termed *aphasia*. It does not depend upon a want or confusion of ideas, because the patient is often perfectly clear as to what he wishes to say, although he cannot say it. It is not due to paralysis of the organs of articulation, since the tongue, lips, and palate can be moved in every direction with the usual facility. It is a deficiency or suspension of the power, either to recall the word needed, or to set in motion the nervous actions required to pronounce it. In the former instance it is called

"amnesic aphasia." The patient cannot say what he wishes, because he cannot recollect the word he wants. For the same reason he is also incapable of writing it. But if the word which he requires be spoken to him, he can repeat it immediately, though in a few seconds it has again escaped him. This disease is an aggravated form of that condition to which many otherwise healthy persons are occasionally liable; namely, that of forgetting for a time a particular word at the moment they wish to use it. In some cases of aphasia the loss of power is so complete that the patient can utter only two or three words, which he employs indiscriminately whenever he speaks at all.

In the second variety of the affection, the patient knows the word he wants, but cannot succeed in articulating it. He can, therefore, express himself by writing perfectly well, but cannot read aloud even what he has written himself. This is called "ataxic aphasia," because it depends not upon an imperfection of memory, but upon a want of power to effect the necessary nervous combinations.

There is no question that the power of language resides somewhere in the cerebral hemispheres, and many observations have tended to locate it more especially in the *convolutions surrounding the lower end of the fissure of Sylvius, and in those of the Island of Reil.* Broca fixes it more especially in the third frontal convolution, surrounding the anterior, ascending branch of the fissure of Sylvius, while others have referred it to the frontal lobe in general. The evidence for this localization of the faculty of language consists in the number of instances in which aphasia more or less complete has been found, on post-mortem examination, to be accompanied by lesions of the brain substance confined to the points indicated. It is often accompanied by hemiplegia of the opposite side of the body, but may sometimes exist independently of any paralytic affection.

According to Broca, it is, as a rule, the third cerebral convolution of the *left hemisphere alone* which is concerned as a nervous centre in the production of articulate language. This conclusion is derived from the fact, which is generally conceded by pathologists, that in the large majority of cases in which aphasia is accompanied by hemiplegia, the hemiplegia is on the right side of the body, the lesion accordingly occupying the left side of the brain. But as aphasia is generally due to occlusion of the middle cerebral artery by an embolism, and as embolism is more likely to occur on the left side than on the right, owing to the different angle at which the vascular branches are given off, this fact may not indicate the exclusive, or even preponderating influence of the left side of the brain in the function of articulate language. Notwithstanding some remarkable cases which would tend to show a special location of this function upon the left side, such as that of chronic left hemiplegia without aphasia, followed in the same individual by a sudden attack of right hemiplegia with aphasia,[1] yet instances of an opposite kind are

[1] Bateman on Aphasia. London, 1870, p. 152.

also so numerous that the physiological question cannot be regarded as settled. We are only certain that aphasia is most frequently produced by lesions occupying the left hemisphere, in the convolutions about the bottom and edges of the fissure of Sylvius; that is, in the parts nourished by branches of the middle cerebral artery.

Special Centres of Motion in the Cerebral Hemispheres.—As a rule, both the white and gray substance of the hemispheres are found to be both insensible and inexcitable under the application of ordinary artificial stimulus; neither sensation nor motion being produced in the living animal by mechanical irritation or injury of these parts. In man, also, it has been repeatedly observed that the substance of the brain, when exposed by accident or disease, gives no indication of sensibility or of motor endowments, if subjected to external irritation.

More careful and extended observations, however, upon the lower animals, have shown that under the influence of galvanic stimulus of a low degree of intensity certain points on the surface of the cerebral convolutions will give rise to definite movements in the muscles of the head, body, and limbs. The fact was first discovered by Fritsch and Hitzig in 1870,[1] and has been subsequently fully confirmed by other observers. The experiments were performed first and most frequently on dogs; afterward on cats, guinea pigs, rabbits, and monkeys; the animals being sometimes stupefied by ether, chloroform, or morphine, sometimes not subjected to any anæsthetic influence.

The general results derived from these experiments, as given by Hitzig, are as follows:

I. One portion of the convexity of the cerebrum, in the dog, is motor; another portion is not motor.

II. The motor portion lies, in general terms, more anteriorly; the non-motor portion more posteriorly.

III. Electrical stimulation of the motor portion produces co-ordinated muscular contraction on the opposite side of the body.

IV. With very weak electric currents, the contractions produced are distinctly limited to particular groups of muscles; with stronger currents, the stimulus is communicated to other muscles of the same or neighboring parts.

V. The portions of the brain intervening between these motor centres are inexcitable by similar means.

These conclusions have been verified by a variety of observations in Germany, France, England, and the United States.[2] The experiments, which are most readily performed on dogs, owing to the large size of the cerebrum, and the comparatively little injury suffered from hemor-

[1] Archiv für Anatomie, Physiologie und Wissenschaftliche Medicin. Leipzig, 1870, p. 300. Hitzig, Untersuchungen über das Gehirn. Berlin, 1874.

[2] Report of a Committee of the New York Society of Neurology and Electrology on the Existence and Localization of Motor Centres in the Cerebral Convolutions. New York Medical Journal, March, 1875, p. 225.

rhage, yield results which are sufficiently uniform to show that they depend upon important physiological conditions. In those performed by the committee of the New York Society of Neurology and Electrology, the animals were etherized and kept more or less completely under the influence of the anæsthetic during the whole course of the experiments. The stimulus employed was a galvanic current from a battery of from 8 to 16 cells, of an intensity just sufficient to be distinctly perceptible, but not painful, when applied to the surface of the tongue. The electrodes were rounded platinum points, fixed at a distance of one millimetre apart. They were applied to the surface of the cerebrum in such a manner as not to wound but only to touch it, and were held in contact with the brain for about one second only at each application. The applications were repeated at short intervals at the same spot for from ten to forty times in succession, in order to make sure that the reactions obtained were not accidental. The results show plainly that there are certain limited spots, on the surface of the cerebral convolutions, at which the application of a faint galvanic current will cause distinct momentary contraction of separate muscles, or groups of muscles, on the opposite side of the body. These spots correspond in all essential particulars with those discovered by Hitzig, and are nearly, though not quite, uniform in location on the two opposite sides, and in different animals.

All the centres of motion for the anterior and posterior limbs are situated, in the dog, in the convolution immediately surrounding the *frontal fissure* (Figs. 161, 162, F), a nearly transverse furrow running outward and forward from the median line, which may be considered as corresponding to the fissure of Rolando in the human brain, but placed farther forward in the dog, owing to the inferior development of the frontal lobe. In a majority of cases, the motor centres for the anterior limbs (3, 4) are situated more in front, near the outer extremity of this fissure; those for the posterior limbs (5, 6) farther backward and inward. At certain points, movements of flexion are produced, at others, movements of extension; sometimes flexion of a single paw alone takes place, sometimes flexion or extension, more or less complete, of a whole limb; and sometimes, at certain spots, there is flexion or extension of the fore and hind limbs together, or partial flexion of one, accompanied by extension of the other. But in the majority of cases, the movements produced are isolated movements of flexion or extension of a single limb.

The centre for flexion of the head on the neck in the median line (1) is in the lateral and anterior part of the convolution situated in advance of the frontal fissure, where this convolution bends downward and outward; that for flexion of the head on the neck, with rotation toward the side of the stimulus, is in a part of the same convolution (2), situated still farther forward and downward, so as to be invisible in a view of the brain taken from above.

The centre of motion for the orbicularis oculi, and, according to Hitzig, for the facial muscles generally, is in a region situated upon the

lateral part of the hemisphere (7, 8, 9), immediately about the supra-Sylvian fissure.

The action of the cerebral convolutions in producing muscular contraction, when this contraction is definite and limited, is always a

Fig. 161.

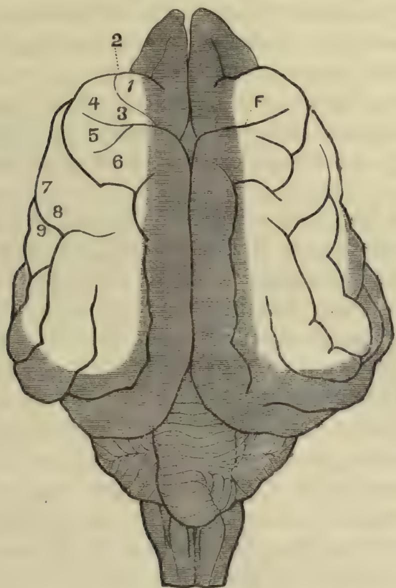
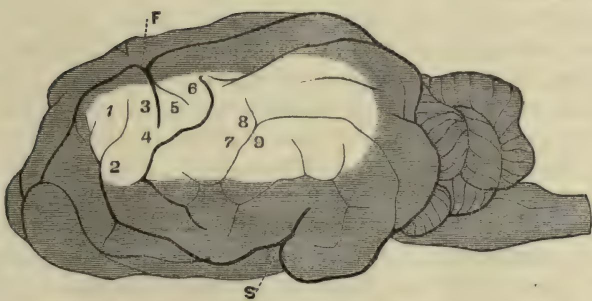


Fig. 162.



BRAIN OF THE DOG.—Fig. 161, view from above; Fig. 162, profile view; showing the centres of motion in the cerebral convolutions. F. Frontal fissure. S. Fissure of Sylvius. The unshaded part is that exposed by the opening in the skull. F. Frontal fissure. S. Fissure of Sylvius. 1. Flexion of head on the neck, in the median line. 2. Flexion of head on the neck, with rotation toward the side of the stimulus. 3, 4. Flexion and extension of anterior limb. 5, 6. Flexion and extension of posterior limb. 7, 8, 9. Contraction of orbicularis oculi, and the facial muscles in general.

crossed action; galvanization of the convolutions, on either side of the brain, exciting movement in the muscles, both of the limbs and face, on the opposite side of the body. On the other hand, galvanization of

the dura mater or other sensitive parts, produces, by reflex action, muscular twitching on the same side of the body.

The existence of these excitable points in the cerebral convolutions does not show that they are nervous centres for the immediate production of voluntary movement. On the contrary, we know that the parts of the brain containing them, and, in some animals, even the whole hemispheres, may be removed and yet the power of movement in the limbs may be preserved. But they are evidently points from which an influence may extend inward toward the central parts of the brain, exciting there the immediate cause of motor action; and this influence is transmitted through the cerebral substance by definite paths, as much so as that passing in the ramifications and fibres of the peripheral motor nerves.

The only doubt which has been entertained in regard to the significance of these experiments is that which attributes the muscular contraction, not to the galvanization of the convolutions themselves, but to a diffusion of the electric current from without inward, and a consequent extension of the galvanic stimulus to the deeper parts of the brain, especially the corpus striatum and ascending fibres of the crus cerebri. But the conditions of the experiment show that this is not the case. When the distance between the two electrodes, and consequently the length of the current traversing the surface of a convolution, is only one millimetre, their application to a particular spot may produce, many times in succession, a definite muscular contraction; and yet their application to other spots not more than five millimetres distant from the first, and equally near the base of the brain, may be entirely without effect.

Furthermore, direct proof of the part taken by the convolutions in the production of these phenomena is supplied by the experiments of Braun[1] and Putnam.[2] In these experiments points were found upon the cerebral convolutions which produced, under the application of electric stimulus, the usual definite muscular contractions. A horizontal section was then made at a depth of one or two millimetres beneath the surface, leaving the flap in place but cutting off the anatomical continuity of brain tissue. The irritation, being then reapplied to the original spot, failed to excite any muscular contraction; but if the flap were turned up and the electrodes applied to the cut surface beneath, a current of similar or slightly increased strength again produced the same movements as before. Repeated trials of this kind, the flap being alternately removed and readjusted, yielded the same results. It is evident, therefore, that when the electrodes, applied to the surface of the uninjured brain, cause movements on the opposite side of the body, this effect is not due to a diffusion of the electric current itself toward the base of the brain, but to a nervous stimulus originating in the convolutions, and thence transmitted inward by the fibres of the white substance.

[1] Centralblatt für die Medicinischen Wissenschaften. Berlin, June 13, 1874, p. 455.

[2] Boston Medical and Surgical Journal, July 16, 1874.

The Cerebral Ganglia.

The corpora striata and optic thalami, from the position which they occupy at the central part and base of the cerebrum, in the course of the ascending fibres of the crura cerebri, must be regarded as nervous centres interposed between the medulla oblongata below and the hemispheres above. According to Henle, the bundles of white substance from the posterior portion of the crus cerebri, on passing into the optic thalamus, spread out in pencil-like tufts of diverging fibres, which become generally distributed throughout the gray substance of the ganglion, and are even mingled in its interior with transverse or interlacing filaments. It is conceded by both Kölliker and Henle that some, or even a considerable proportion, of these fibres terminate in the gray substance; while a portion, or perhaps other fibres originating in the gray substance, pass outward again, from the anterior and lateral parts of the thalamus, to continue their course upward to the cerebral convolutions.

In the corpus striatum, the relation of the fibres to the gray substance is, in general, the same as in the thalamus; that is, they are derived from the ascending bundles of the crus cerebri and terminate in the gray substance of the ganglion. The difference between the two bodies is that in the thalamus the mixture of the fibres with the gray substance is more intimate and uniform throughout, while in the corpus striatum the fibres are arranged in distinct bundles, readily visible to the naked eye, which only disappear, by the dispersion and termination of their filaments, at the distance of about one millimetre from its outer edge; so that the ganglion is bordered externally at this situation by a thin layer of gray substance in which no white striations are to be seen. In the corpus striatum, as in the optic thalamus, there are also bundles of fibres, according to the observations of Kölliker, which at certain levels pass from the gray matter of the ganglion into the white substance of the hemispheres. Both the corpus striatum and optic thalamus contain nerve cells with ramified prolongations, some of which closely resemble the finest nerve fibres with which they are mingled, and with which many anatomists believe them to be continuous.

The exact physiological function of the cerebral ganglia, as distinguished from the hemispheres proper, is not precisely determined. It is plain that they exert some influence, of an intermediate character, between the action of the cerebral hemispheres above and the direct transmission of motor and sensitive stimulus to or from the parts below. They have both been found to be, like the hemispheres, insensible to ordinary mechanical irritation, unless this be applied so deeply as to reach the fibrous bundles of the crura cerebri in their inner and deeper parts. They cannot be extirpated or extensively injured without at the same time cutting off more or less completely the connection of the hemispheres with the peripheral nervous system; but they may be removed at the same time with the hemispheres, in some of the lower

animals, and yet the power of motion and of sensibility may be retained to a considerable extent.

It is certain, however, from the known facts of pathology, that their influence is an important one, since, in man, lesions of these ganglia are almost always followed by more or less complete *hemiplegia* on the opposite side of the body. In general terms, the effect of cerebral hemorrhage, whether from injury or disease, may be said to vary according to its location; hemorrhage upon the surface of the hemispheres producing coma, that in the cerebral ganglia causing hemiplegia. The usual significance attached to the term "hemiplegia" is that of loss of voluntary motion on one side, while a corresponding loss of sensibility is designated as *hemianæsthesia.* In cases of lesion of the cerebral ganglia or adjacent parts, the loss of motion is usually the most prominent symptom, hemianæsthesia being either entirely absent or disappearing rapidly, while the motor paralysis lasts a longer time. On the other hand, hemianæsthesia may continue after the power of motion is recovered, and it may also be produced in animals by lesions of the brain without being accompanied by any muscular paralysis.

Attempts have been repeatedly made by various authors to locate more distinctly the physiological acts of sensation or motion in one or the other of the cerebral ganglia separately; but thus far these attempts have not been so successful as to command general assent. The most exact experiments in regard to sensibility are those of Veyssière,[1] who operated by introducing into the brain of the dog a slender trocar armed with a spring, which could be expanded at the bottom of the wound and thus produce, by rotation of the instrument, a lesion of the deeper parts of the brain without serious injury of the more superficial portions. After study of the symptoms caused by the operation, the animal was killed, and the exact location of the injury ascertained. The observer found by this means that hemianæsthesia, either alone or accompanied by more or less paralysis of motion, was produced by lesions of the cerebral ganglia and the white substance included between them; but that it was the white substance of the internal capsule which was most constantly affected in these cases. The gray substance of the cerebral convolutions, as well as that of the cerebral ganglia, might be extensively injured without causing loss of sensibility; but this effect was produced in proportion to the extension of the injury to the internal capsule and the commencement of the expansion of radiating fibres derived from it.

The above experiments and observations do not show that the physiological functions, either of sensibility or voluntary motion, are seated in the cerebral ganglia or the internal capsule. The paralysis of motion and sensation resulting from injury to these parts is due evidently, in great measure, to the shock communicated, through descending fibres, to other parts of the brain below; since, as in several of Veyssière's

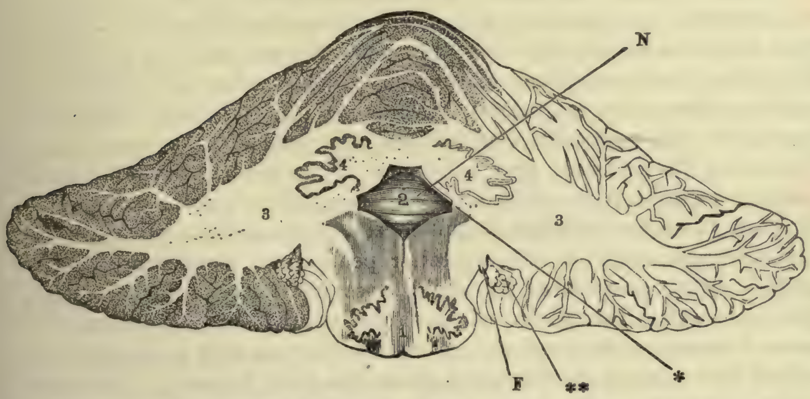
[1] Recherches sur l'Hemianæsthésie de cause cérébrale. Paris, 1874.

experiments, a hemiplegia or hemianæsthesia, following laceration of the brain substance, may disappear within a few days, or even in twenty-four hours, though the mechanical injury be not yet repaired. While therefore we cannot say that either of the cerebral ganglia are the physiological organs of sensation or motion, yet their injury, both in animals and in man, generally produces, as its immediate result, hemiplegia or hemianæsthesia, either singly or combined, on the opposite side of the body.

The Cerebellum.

The cerebellum, although in man and the quadrupeds much inferior in size to the cerebrum, consists, like it, of a folded layer of gray matter surrounding the mass of white substance which forms its internal portion. The cortical layer of gray substance is only about one-half as thick as that of the cerebral hemispheres; being nowhere over 1.5 millimetre in thickness. But the convolutions of the cerebellum are more compactly arranged than those of the cerebrum, and penetrate into its substance in the form of thin, closely adjacent laminæ; so that it contains a comparatively large quantity of gray matter in proportion to its mass. In the white substance of the cerebellum on each side, not far from the median line, there is an isolated deposit of gray matter in the

Fig. 163.



VERTICAL TRANSVERSE SECTION OF THE HUMAN CEREBELLUM AND MEDULLA OBLONGATA, a little behind the pons Varolii; posterior portion.—1. Medulla oblongata, showing the nucleus of the olivary bodies. 2. Fourth ventricle. 3, 3. White substance of the cerebellum. 4, 4. Corpus dentatum of each side. (Henle.)

form of a thin lamina, folded in irregular, tooth-like convolutions, whence its name of *corpus dentatum.* This lamina is everywhere closed on its external lateral aspect, but presents an opening at one point toward the median line. It seems to occupy, in the cerebellum, a place analogous to that of the cerebral ganglia above, and to that of the olivary nuclei in the medulla oblongata.

The gray matter of the cerebellar convolutions is penetrated by fibres

coming from the interior white substance, and contains nerve cells of various form and size. The most characteristic are flask-shaped cells, arranged in a single or rarely in a double row; the rounded extremity of each cell being directed inward, the pointed extremity outward. According to Kölliker and Henle, the cells usually give off prolongations in two opposite directions; that which passes inward toward the white substance being unbranched and resembling the axis-cylinder of a nerve fibre, while that which passes outward toward the surface of the convolution divides into numerous fine ramifications.

The cerebellum is connected with the rest of the cerebro-spinal axis by, 1st, the fibres of the posterior peduncles, or *restiform bodies*, which come from the posterior and lateral parts of the medulla oblongata, to radiate in the white substance of the cerebellum; and 2d, by those of the anterior peduncles, or *processus e cerebello ad corpora quadrigemina*, which originate from the cerebellum nearer the median line than the termination of the restiform bodies, and thence pass upward and forward, joining the longitudinal tracts of the posterior part of the tuber annulare and crura cerebri. The two lateral halves of the cerebellum are furthermore connected with each other by, 3d, the fibres of the middle peduncles, which originate from the white substance on each side, then pass forward and downward to meet in front upon the under surface of the tuber annulare, forming the arched commissure of the *pons Varolii.*

Physiological Properties of the Cerebellum.—The general result of experimental operations upon the cerebellum shows that the surface of this organ is inexcitable by ordinary means, and that its mechanical irritation gives no evidence of sensibility. Flourens, Longet, Vulpian, and experimenters in general, have recognized the fact that neither sensation nor muscular contractions are produced by touching or wounding the external gray substance of the cerebellum; while in its deeper portions both excitability and sensibility become manifest, in proportion as the irritation is applied nearer the medulla oblongata and the commencement of the cerebellar peduncles. Furthermore, its removal, either in part or in whole, does not destroy nor essentially diminish either the power of sensation or that of movement. The senses remain active, and the mental faculties are still unchanged, provided the cerebral hemispheres have not been injured. Operations upon this part of the brain are more difficult to perform than those upon the cerebrum, and are much more liable to produce a fatal result. This, however, does not seem to depend upon any direct influence of the cerebellum upon the more vital functions, but is due to its deeper position, the difficulty of exposing it without causing too much hemorrhage, and especially its proximity to the medulla oblongata. If injury from these causes be avoided, the organ may be extensively wounded or even totally removed without causing death. One-half or two-thirds of it have often been taken away without causing death; and in one of the experiments of Flourens, a fowl lived for more than four months after its complete extirpation.

Aside from the particulars above mentioned, experiments which consist in mutilation or removal of the cerebellum have yielded very uniform results of a striking character, and not similar to those caused by injury to other parts of the brain. These effects were first described by Flourens in 1842;[1] and notwithstanding the great activity of research upon the nervous system since that time, the results obtained by him have been uniformly corroborated in all essential particulars by subsequent observers. The phenomena, which are of a similar nature in different species of animals, have been seen, by Flourens or others, in the pigeon, fowl, duck, turkey, and other birds; and, among quadrupeds, in the dog, the cat, the mole, the rat, and the guinea pig.

The effect produced by destruction or removal of the substance of the cerebellum consists in a peculiar disorder of the movements of the body and limbs, from want of harmony in their muscular action. The power of associating the contractions of different muscles, in such a way as to produce co-ordinated movements, is lost or impaired in proportion to the injury inflicted upon the nervous centre. If in a living pigeon the cerebellum be exposed, and a portion of its substance removed, the animal exhibits at once a characteristic uncertainty in the gait, and in the movement of the wings. If the injury be more extensive, the bird loses altogether the power of flight, and can walk, or even stand, only with difficulty. This is not owing to any actual paralysis, for the movements of the limbs are often quite rapid and energetic; but is due to a deficient control over the muscular contractions, similar to that seen in a man in a state of intoxication. The movements of the legs and wings, though forcible, are confused and blundering; so that the animal cannot direct his steps to any particular spot, nor support himself in the air by flight. He reels and tumbles, but can neither walk nor fly.

The senses and the intelligence are at the same time unimpaired, and this circumstance causes a striking difference between the phenomena produced by removal of the cerebrum, and those following removal of the cerebellum. If these two operations be done upon different pigeons, and the two animals placed side by side, the first pigeon, from which the cerebrum only has been removed, remains standing firmly upon his feet, in a condition of complete repose; and when compelled to stir, he moves sluggishly and unwillingly, but otherwise acts in a perfectly natural manner. The second pigeon, on the other hand, from which the cerebellum only has been taken away, is in a constant state of agitation. He is easily excited, and frequently endeavors, with violent struggles, to escape from one place to another; but his movements are sprawling and unnatural, and no longer under the effectual control of the will. If the entire cerebellum be destroyed, the animal is incapable of assuming or retaining any natural posture. His legs and wings are

[1] Recherches Expérimentales sur les Propriétés et les Fonctions du Système Nerveux. Paris, 1842, pp. 37, 53, 102, 133.

agitated with ineffectual movements, which are evidently voluntary in character, but are at the same time irregular and confused.

The direct inference which may be derived from these phenomena is that the power of co-ordination or association of voluntary movements of the body and limbs resides in the cerebellum as a nervous centre, and that this power is accordingly lost or impaired by injury of its substance. It is evident that such a power really exists under some form in the nervous system. No natural co-ordinated movements are effected by the independent contraction of separate muscles, but always by a number of muscles, or groups of muscles, acting in harmony with each other. The extent and variety of this muscular association vary in different classes of animals. They are very considerable in birds and quadrupeds as compared with fish and reptiles, and reach in man their highest grade of development. Even in maintaining the ordinary postures of standing or sitting, many different muscles are brought into action together, in each of which the degree of contraction must be accurately proportioned to that of the others. In the motions of walking and running, or in the still more delicate movements of the hands and fingers, this harmony of action is indispensable to the efficiency of the muscular apparatus.

Notwithstanding the fact that this power of co-ordination is invariably disturbed by injuries of the cerebellum, it is doubted by some writers whether it can be strictly attributed, as a physiological function, to this particular part of the nervous system. The grounds upon which this doubt is based áre twofold; first the subsequent recovery of the power of co-ordination by animals after injury or partial removal of the cerebellum, and secondly, the results of certain pathological observations in the human subject.

I. *Restoration of the Co-ordinating Power in Operated Animals.*— It is certain that animals may be affected, after partial extirpation of the cerebellum, with well marked loss of co-ordinating power, and that they may, in some instances, subsequently recover this power without regeneration of the lost nervous substance. This recovery was observed by Flourens in the fowl and in the pigeon, and has been seen by Flint[1] in the pigeon after removal of about two-thirds of the whole mass of the cerebellum. We have also met with four instances of the same kind. In the first, about two-thirds of the cerebellum was taken away by an opening in the posterior part of the cranium. Immediately afterward, the pigeon showed all the usual effects of the operation, being incapable of flying, walking, or even of standing still, but only reeled and sprawled in a perfectly helpless manner. In five or six days from that time, he had regained a very considerable control over the voluntary movements, and at the end of sixteen days his power of muscular co-ordination was so nearly perfect, that its deficiency, if any existed, was imperceptible. He was then killed; and on examination, it was found that his cerebel-

[1] The Physiology of Man; Nervous System. New York, 1872, p. 367.

lum remained in nearly the same condition as immediately after the operation; about two-thirds of its substance being deficient, with no regeneration of the lost parts. The accompanying figures show the appearances in this brain as compared with that of a healthy pigeon.

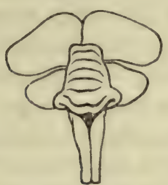
Fig. 164.

Brain of Healthy Pigeon—Profile view.—1. Cerebral hemisphere. 2. Optic tubercle. 3. Cerebellum. 4. Optic nerve. 5. Medulla oblongata.

Fig. 165.

Brain of Operated Pigeon—Profile view—showing the mutilation of the cerebellum.

Fig. 166.



Brain of Healthy Pigeon—Posterior view.

Fig. 167.

Brain of Operated Pigeon—Posterior view—showing the mutilation of the cerebellum.

In the three remaining cases the quantity of nervous substance removed amounted to about one-half the mass of the cerebellum. The loss of co-ordinating power, immediately after the operation, though less complete than in the preceding instance, was perfectly well marked; and in little more than a fortnight the animals had nearly or quite recovered the natural control of their motions, so far as could be seen while they were kept under observation.

It is evident that in these cases, if the cerebellum be really the seat of a physiological co-ordinating power, there are two effects produced by the operation, which should be carefully distinguished from each other. The first of these effects is the shock due to the *sudden injury of the cerebellum as a whole.* This effect is temporary, and may be recovered from in time, provided the animal be sufficiently strong to survive the immediate mechanical lesion. The remaining effect is that due to *the loss of nervous substance;* and this effect must of course be permanent, unless the nervous matter be regenerated. In the cases detailed above, the greatest amount of disturbance seems to have depended upon the sudden injury to the nervous centre as a whole; and the animals recovered, to a great extent, their power of co-ordination, notwithstanding that from one-half to two-thirds of the substance of the cerebellum was permanently lost.

The recovery of a nervous function, after permanent loss of nervous substance, is not peculiar to the cerebellum. Flourens has observed the same thing in regard to the cerebral hemispheres in the pigeon; the intellectual and perceptive faculties being totally suspended immediately after partial removal of the hemispheres, but again restored after the lapse of several days. But this restoration only takes place where the removal of the nervous centre is partial; and in the cerebellum, as well as in the cerebrum, after complete extirpation, the loss of function is a permanent one. In the experiment of Flourens, where a fowl lived for four months after entire removal of the cerebellum, there was no recovery of co-ordinating power.

It is to be remembered that birds and other animals, when confined to the limited space of a laboratory, have no opportunity of exercising the more complicated and active movements natural to them in a condition of freedom; and accordingly, they might not show any great deficiency of muscular co-ordination while in confinement, though they might still be incapable of executing all the movements of natural flight. The simpler motions may continue to be performed with only a part of the cerebellum remaining; but we are not sure that, even in these cases, a portion of the co-ordinating power, corresponding with the destruction of nervous substance, has not been permanently lost.

II. *Pathological Observations in the Human Subject.*—The same remark will apply to the pathological observations in man which have been sometimes considered as neutralizing the result of experiments. These are mainly cases in which lesions of the cerebellum, more or less extensive, have existed without recorded disturbances of co-ordination similar to that produced in animals by mechanical injury of the part. In a large majority of these instances the patients were confined to a sick-room, and in many of them to the bed; consequently there could be no opportunity of observing a want of natural co-ordination in the more complicated movements, if any such existed. A patient, also, in whom the loss or diminution of a motor nervous function comes on gradually, accommodates himself to it by abstaining from the attempt to perform movements of which he is incapable, and confines himself to those which he is still able to perform. Furthermore, in many cases of disease of the cerebellum, symptoms of want of co-ordinating power have been distinctly noticed and recorded.

The data derived from *comparative anatomy* show a general correspondence in the development of the cerebellum and the variety and complication of muscular action. In fish, as a rule, it is of good size compared with other parts of the brain; and although direct progression in this class is accomplished by a comparatively simple mechanism, namely, the lateral flexion and extension of the spinal column with its expanded fins and tail, yet their movements through the water or in leaping out of it, while pursuing and taking their prey, are remarkably rapid and vigorous, and are promptly varied in any direction. In the frog, on the other hand, the movements of progression consist of little

else than straightforward flexion and extension of the posterior limbs; and the cerebellum is exceedingly small, much inferior in size to that of fishes, and forms only a thin narrow ribbon of nervous matter stretched across the upper part of the fourth ventricle. In the chelonia, or turtles, the movements of the body are accomplished by the consentaneous action of the anterior and posterior limbs, and those of the head and neck are also much more varied than in the frog, while the cerebellum exhibits a corresponding increase of development. In the alligator and allied species, whose motions approximate more closely to those of the quadrupeds than is the case with other reptiles, the cerebellum is also larger in proportion to the remaining parts of the brain. In birds, in quadrupeds, and in man there is a very evident increase in the size and convolutions of the cerebellum, corresponding with the greater variety and delicacy of movements which they are capable of performing. These facts are not decisive in determining the physiological function of this portion of the brain, since other nervous endowments also vary in their degree of development in different animals and in man; but they show that the assumption of a co-ordinating power in the cerebellum is not at variance with the comparative anatomy of the nervous system.

Everything which we know with certainty, therefore, in regard to the cerebellum, indicates its close connection with the power of co-ordination for the movements of the body and limbs. It cannot be regarded as exclusively presiding over this function; since there is strong evidence that the posterior columns of the spinal cord are in great measure devoted to the same purpose, and their morbid alteration necessarily induces, in man, the disease known as locomotor ataxia. But the posterior columns of the cord form by their divergence, at the level of the fourth ventricle, the inferior peduncles of the cerebellum. The cerebellum accordingly is a highly developed and convoluted nervous centre, placed at the upper extremity of the cord, and communicating, by tracts of white substance, with its posterior columns. The spinal cord itself is, of course, essential to the co-ordinated motions of the body, arms, and legs, since its posterior columns are for them the direct agents of control and communication; but the cerebellum may also be regarded as a focus or nervous centre of reflex action for all the more vigorous and complicated movements of the trunk and limbs.

The Tuber Annulare.

The tuber annulare is an isthmus, which makes connection between the remaining parts of the encephalon above, and, through the medulla oblongata, with the spinal cord below. It may be described in general terms as constituted, 1st, by longitudinal tracts of white substance, the prolongation of the anterior pyramids of the medulla oblongata, which pass through it in a nearly straight course, becoming continuous above with the crura cerebri; 2d, by transverse bundles of white substance coming from the two sides, and encircling it with the superficial

band of arched fibres, known as the pons Varolii, or great commissure of the cerebellum; and 3d, by a deposit of gray substance contained in its anterior, and more or less mingled with its other portions. The tuber annulare is, therefore, like the other central masses of the encephalon, at the same time a channel of communication between the interior and the exterior, and a nervous centre with special endowments of its own.

In the most superficial portions of the pons Varolii, the transverse bundles of nerve fibres are closely packed together, without any perceptible admixture of nerve cells. The deposit of gray substance commences, however, according to Henle, at a short distance below the surface, occupying minute spaces between the transverse bundles, and containing stellate nerve cells. Beneath the superficial transverse bundles of the pons come the longitudinal tracts of pyramidal nerve fibres, and beneath these again a deeper layer of transverse commissural fibres. The deposit of gray matter in the pons is still more abundant in its deep than in its superficial layer; often alternating, according to Henle, with the transverse bundles, in interspaces of $\frac{1}{2}$ millimetre in thickness. It also fills a space about 2 millimetres wide, on each side the median line, between the two pyramidal tracts of white substance.

Physiological Properties of the Tuber Annulare.—In the tuber annulare the phenomena both of excitability and sensibility, under artificial irritation, become much more marked than in the great centres of the cerebrum and cerebellum. According to Longet, a galvanic stimulus, when the electrodes are passed into the substance of this organ, produces distinct convulsive movements even in recently killed animals, although its external surface does not appear to be excitable by similar means either in front or behind. Very slight irritation of its posterior surface has been found, by both Longet and Vulpian, to give rise in the living animal to indications of pain; but this effect may be partly due to the contiguity of the sensitive nerve-roots which traverse the nervous substance in this situation. Excitability and sensibility are also manifested on irritating the crura cerebri, between the tuber annulare and the cerebral ganglia.

The nature of the physiological actions taking place in the tuber annulare, as a nervous centre, can only be studied by observing the effects produced by its injury or removal, in comparison with other parts of the encephalic mass. It is seen that the cerebrum and cerebellum may be taken away, either together or separately, without destroying the evidences of sensibility or the power of motion. According to the experiments of both Longet and Vulpian, the cerebral hemispheres, the cerebellum, the corpora striata, the optic thalami, and the tubercula quadrigemina may all be removed, in dogs and rabbits, and yet the signs of sensibility and the power of motion in the limbs continue to exist; and, if the cerebellum remain, the normal attitude of the body and limbs, and even the power of progression, may still be maintained.

The manifestations of these nervous functions, however, are so much

diminished after extirpation of the cerebral hemispheres, that some writers have suspected that they might belong to the category of unconscious and involuntary reflex actions. Longet and Vulpian, on the other hand, insist upon the fact, observed by both, that after removal of the whole brain, with the exception of the tuber annulare and medulla oblongata, irritation of the external parts or of a sensitive nerve will produce, in dogs and rabbits, cries which are evidently the expression of a conscious sensation. This alone shows that the animals after such a mutilation may be still capable of feeling pain; and, according to Vulpian,[1] after extirpation of the hemispheres and the cerebral ganglia in the rat, movements of the head and limbs were not only produced by pinching the integument, but blowing suddenly upon one of the ears caused shaking of the head, accompanied by winking of the eyes; showing that the animal was still sensitive to ordinary tactile impressions, as well as to those of a painful character. The same experimenter has found that in a rat, after the above operation, a hissing sound made by the lips excited repeatedly distinct signs of agitation. From these facts it can hardly be doubted that sensations are actually perceived by the animal so long as the tuber annulare remains uninjured.

There is no evidence, however, that in these cases there is anything more than the simple sensation, without conscious recognition of its origin or significance. So far as we can judge, the animal under these circumstances may be capable of feeling pain, but not of understanding the cause by which it was produced. He may be conscious of the sensations of light or of sound, as existing in himself, without referring them to any external source. This is the full extent of sensibility, as it can be supposed to exist in the tuber annulare.

A similar limitation must be placed on the action of the voluntary muscles so far as it is excited by the tuber annulare. These motions have the appearance of volition, so far as they consist in attempts to maintain or recover the natural attitude, or in those of progression; but it is not a volition which has any intelligent understanding of its purpose. It follows immediately upon the receipt of the sensation which excites it, and is therefore a reflex action; but it differs from the reflex action of the spinal cord mainly in the fact, that it is accompanied or preceded by a conscious sensation.

The evidence thus far in our possession goes to show that the tuber annulare is especially connected with reflex actions *of an emotional and instinctive character*. These actions differ from those connected with the mental faculties in being comparatively little under the control of the judgment or the will, and in being directed by an unreasoning impulse, where the act follows immediately upon the receipt of the sensation. To this class belong the purely instinctive acts performed by animals or man, in which there is no direct recognition of their ulti-

[1] Leçons sur la Physiologie du Système Nerveux. Paris, 1866, p. 543.

mate object, but only of the immediate stimulus upon which they depend. All the emotions, and the expressions to which they give rise, are nervous phenomena of this kind. The feelings of cheerfulness or depression, satisfaction, hilarity, or displeasure, are expressed, whenever they reach a certain degree of intensity, by tears or laughter, by inarticulate sounds, attitudes or movements of the body, which, though not intentionally calculated to produce that effect, are at once understood by all who see or hear them. In man, certain diseases of the brain induce a condition in which the emotional phenomena are much more easily excited than in health, either from an undue activity of the nervous centre in which they are located, or from the diminished influence exerted over them by the cerebral hemispheres. In these instances, the individual is moved to anger, laughter, or tears on the most trivial occasions, and from causes which would not produce such an effect in a condition of health; the feelings thus expressed being quite uncontrollable for the time, although the patient may be conscious that they have no reasonable motive.

The action of the tuber annulare, as the centre of the emotional impulses, is no doubt closely connected with its influence over the attitude and locomotion. The manner in which these two functions are performed, even in man, takes a great share in the manifestation of the emotions, and in many of the lower animals forms the principal means by which they are expressed. The normal postures of the body and limbs and the movements of progression, although they are still possible after destruction of the cerebral hemispheres and ganglia, are at once abolished, according to Vulpian, if the tuber annulare be removed or extensively injured.

There is no doubt, also, that the other nervous faculties which have been enumerated as connected with the tuber annulare come to an end as soon as this organ is subjected to mutilation. With the destruction of the tuber annulare, according to the general testimony of experimenters, all indications of sensibility and volition disappear, and the animal body is reduced to the condition of a helpless and unconscious machine, in which the functions of respiration and circulation, with certain other involuntary reflex phenomena, are the only remaining manifestations of nervous action.

The Medulla Oblongata.

The medulla oblongata is distinguished from the spinal cord, of which it is a continuation, not only by its external form, but also by the different arrangement both of the bundles of nerve fibres and of the gray substance in its interior.

In the spinal cord, the anterior, middle, and posterior columns of white substance all consist mainly of parallel fibres running in a longitudinal direction; while there is a narrow band of transverse fibres, the white commissure, at the bottom of the anterior median fissure. In the medulla oblongata, a much larger number of horizontal and oblique

fibres make their appearance, passing from one side to the other. The greater part of these fibres come from the continuations of the lateral and posterior columns, and from the posterior horns of gray matter, whence they pass forward and inward, and cross each other on the median line at the place previously occupied by the white commissure. The increasing number of these interchanging fibres, and the fact that they cross the median line in bundles of considerable size, and in an oblique direction from below upward, produce the conformation visible at the anterior surface of the medulla oblongata, and known as the *decussation of the pyramids*. After crossing from one side to the other, the fibres again gradually take a longitudinal direction, and it is on this account that the pyramids increase in size from below upward. The pyramids accordingly consist of fibres which are derived from the lateral and posterior columns of the opposite side of the cord. They are not the continuation of the longitudinal tracts which form the anterior columns below; these columns, on the contrary, diminishing rapidly in size from within outward, until they disappear almost completely above the level of the decussation of the pyramids. Thus the decussation of the pyramids represents that of all the remaining longitudinal fibres of the spinal cord, so far as it takes place in the medulla oblongata.

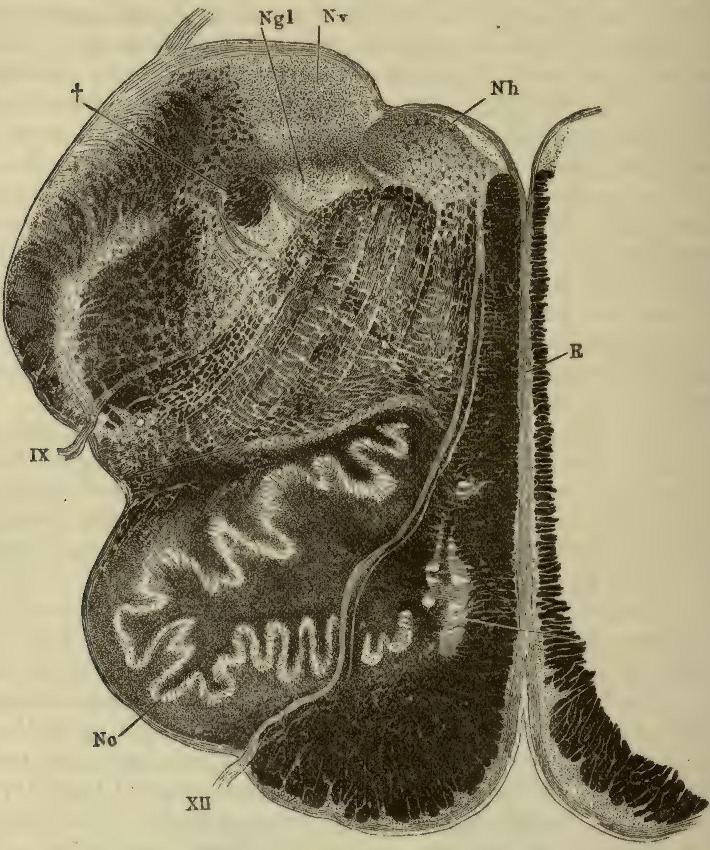
The longitudinal fibres of the posterior columns also diminish considerably in number in the medulla oblongata, as shown by Henle, owing to their taking a horizontal direction, forward and inward, to reach the decussation of the anterior pyramids; while the remaining longitudinal fibres of these columns pass into and through the restiform bodies to the white substance of the cerebellum.

The arrangement of the *gray substance* in the medulla oblongata is also different from that presented in the spinal cord. In the first place, according to the observations of Kölliker, it increases in quantity from below upward. Secondly, the central mass of gray substance, which in the cord surrounds the central canal, and sends out on each side the anterior and posterior horns, recedes in the medulla oblongata farther and farther backward; the posterior horns spreading out laterally, and the remainder occupying the space between them. The posterior median fissure also becomes gradually shallower and wider by the divergence of the posterior columns; and the central canal approximates the posterior wall of the medulla, finally opening upon its surface at the lower part of the fourth ventricle. The gray substance of the medulla oblongata is thus uncovered posteriorly, and forms a layer spread out laterally, on each side of the median line, immediately beneath the floor of the fourth ventricle. It extends forward, without any complete interruption, beneath the whole length of the fourth ventricle and the aqueduct of Sylvius; and it is this layer of gray substance which gives origin, at various points, to the fibres of all the cranial nerves, excepting the olfactory and the optic.

Thirdly, the medulla oblongata is distinguished by the appearance, in its interior, of other deposits, or nuclei, of gray substance, detached

from those belonging to the spinal cord. The most marked of these is the *olivary nucleus;* a convoluted lamina about one-third of a millimetre in thickness, occupying the interior of the olivary body on each side, just below the inferior border of the pons Varolii.

Fig. 168.



TRANSVERSE SECTION OF HUMAN MEDULLA OBLONGATA, at the lower part of the fourth ventricle.—No, Olivary nucleus. R, Raphe, at the median line. Ngl, Nucleus of the glosso-pharyngeal nerve. Nv, Nucleus of the pneumogastric nerve. Nh, Nucleus of the hypoglossal nerve. IX, Roots of the glosso-pharyngeal nerve (9th pair) at their point of emergence from the medulla. XII, Roots of the hypoglossal nerve (12th pair) at their point of emergence from the medulla. Magnified 8 diameters. (Henle.)

In transverse sections, near its upper or lower extremity, the olivary nucleus appears completely closed, but a section through its middle shows a gap toward the median line. It forms, therefore, an ovoid sac, with its long diameter parallel to the axis of the medulla, and an opening at its middle directed inward. Through this opening bundles of nerve fibres penetrate from the white substance of the medulla, and,

after filling the space inclosed by its convoluted wall, pass through it, and spread out laterally in a divergent direction.

Physiological Properties of the Medulla Oblongata.—The simplest examination of the medulla oblongata shows that its physiological properties are more distinctly marked than those of any other part of the encephalic mass. It is both sensitive and excitable to a high degree, especially in its posterior portions. Artifical irritation, by mechanical or galvanic stimulus, causes at once a painful sensation, provided the rest of the brain be uninjured, and in the recently killed animal produces general convulsive movements of considerable intensity. These effects are due to the irritability of the longitudinal fibres connecting the medulla with the spinal cord, and to the roots of the sensitive and motor cranial nerves which take their origin from this part of the encephalic mass. Since the medulla is the only bond of nervous communication between the brain and the spinal cord, its section at any point also destroys voluntary motion and sensibility throughout the body and limbs.

Action of the Medulla as a Nervous Centre.—The various deposits of gray substance in the interior of the medulla, and their connection with nerves of widely different distribution and functions, are the peculiar features of its anatomical structure. The results of experiment show that the reflex actions taking place in this part of the nervous system are also of a special and distinctive character.

The most important of these actions is connected with *respiration.* So long as the medulla oblongata is left uninjured, although the cranium be emptied of all the other nervous centres, the movements of respiration and circulation go on without essential modification. But if the medulla be destroyed, respiration ceases instantaneously. This effect may be produced, without injuring other parts of the brain, in dogs or other warm-blooded animals, by introducing a steel instrument from behind, between the edges of the occipital foramen and the first cervical vertebra, carrying it forward in the median line until its point rests upon the basilar process of the occipital bone. It is then moved from side to side in such a way as to break up the substance of the medulla oblongata, when all the movements of respiration are at once arrested. The circulation continues, and the pulsations of the heart are even increased for a time in force and frequency; but as the deficiency of aeration in the blood becomes more marked, the circulation is gradually retarded and after several minutes comes to an end. The effect of this operation upon the two functions of circulation and respiration is very different. The circulation is interfered with and finally suspended in a secondary manner, and only because the blood is no longer arterialized; respiration is abolished instantaneously, as the immediate result of the destruction of the medulla oblongata.

The medulla is, therefore, the most important nervous centre in the brain for the immediate preservation of the vital functions, and the only one whose injury or removal produces at once a fatal result.

In man, quadrupeds, and birds, it is a vital point; since in them the function of respiration, over which it presides, is necessary for the continuance of life from one moment to another.

The fact that sudden death may be produced by injury of the cerebro-spinal axis in this region was known to Galen, who described the method of killing an animal by section of the spinal cord "at the upper cervical vertebræ." The respiratory movements of the chest and abdomen are however necessarily arrested by section of the cord anywhere above the third cervical vertebra, since this paralyzes at once both the diaphragm and the intercostal muscles. But movements of inspiration, simultaneous with those of the chest and abdomen, are also performed by the glottis; and in most of the quadrupeds there is at the same time an expansion of the nostrils, all associated with each other in the act of respiration. If the spinal cord be divided at the third cervical vertebra the movements of the chest and abdomen cease, but those of the glottis and the nostrils continue, since the nerves supplying these parts are still in communication with the medulla oblongata. Destruction of the medulla itself, on the other hand, arrests at the same instant all movements of respiration, both in the trunk, the glottis, and the face. It is, therefore, a centre from which the respiratory apparatus in general derives its stimulus.

The more exact location of this centre was investigated by Flourens[1] by making transverse sections of the medulla at different parts of its length, and observing the effect produced upon respiration. The result showed that injuries of this kind, inflicted just behind the point of emergence of the pneumogastric nerves, destroyed at once all the movements of respiration together. Below this point the movements of the chest and abdomen were stopped, but those of the nostrils and glottis continued; above it the movements of the nostrils were arrested, while those of the chest and abdomen went on.

Similar experiments performed by Longet show that the respiratory centre does not extend through the entire thickness of the medulla; since either the anterior pyramids in front or the restiform bodies behind may be destroyed without putting a stop to respiration; while a lesion passing through the intermediate layer at once causes its suspension. Flourens subsequently[2] limited the position of this centre still more closely, and found that in rabbits it occupies a space of about 2.5 millimetres on each side the median line, situated at the lower end of the fourth ventricle, a little in advance of the divergence of the posterior pyramids, and just at the point of gray substance formed by the *ala cinerea*. A section of the medulla at this spot, with a double-edged knife only 5 millimetres wide, or its perforation at the same point with a sharp-edged canula not more than 3 millimetres in

[1] Recherches Expérimentales sur les Propriétés et les Fonctions du Système Nerveux. Paris, 1842, pp. 196–204.

[2] Comptes Rendu de l'Académie des Sciences. Paris, 1858, tome xlvii. p. 803.

diameter, caused immediate stoppage of the respiration; while this effect was not produced by similar injuries inflicted either above or below. This spot, which contains the nervous centre of the movements of respiration, corresponds in level, in front of the medulla oblongata, with the upper end of the decussation of the anterior pyramids, or the lower extremity of the olivary bodies, and is somewhat below the apparent origin of the pneumogastric nerves.

Respiration accordingly is an act consisting of various associated movements, which have their nervous centre in the medulla oblongata. The respiratory movements themselves are completely involuntary in character; for although those of the chest and abdomen may be for a short time increased in frequency, the surplus movements thus performed are not necessary to respiration, and soon produce a fatigue which prevents their continuance. Respiration goes on with its natural rhythm, and entirely unaccompanied by fatigue, under the influence of the medulla, from the first moment of birth and without any necessary consciousness of its existence. If arrested by a voluntary effort, the internal stimulus which prompts the movement grows gradually stronger, until the will is no longer capable of resisting its demands. As soon as the voluntary resistance is overcome or discontinued, the respiratory movements recommence by the independent action of the medulla oblongata.

The action of the medulla in respiration is one of a reflex nature. The impression by which it is called out has its origin in the partial want of arterialization of the blood, and especially in the commencing accumulation of carbonic acid in the lungs and in the tissues. In normal respiration, this impression is sufficient to excite the reflex action of the medulla without producing a conscious sensation; and on the renewal of the air in the lungs by inspiration, the impulse is satisfied, the muscles relax, and expiration is accomplished by the passive collapse of the lungs and thorax. In a few seconds the previous condition recurs and the actions are repeated as before, causing in this way the regularly alternating movements of inspiration and expiration.

Since the acts of inspiration are performed partly by the diaphragm and partly by the intercostal muscles, they will be differently modified by injuries or lesions of the nervous system, according to the spot at which they are situated. If the spinal cord be divided or compressed in the lower cervical region, all the intercostal muscles are necessarily paralyzed, and respiration is then performed only by the diaphragm. If the phrenic nerve, on the other hand, be divided, the diaphragm alone is paralyzed, and respiration is performed altogether by the rising and falling of the ribs. If the injury inflicted upon the spinal cord be above the origin of the third cervical nerve, both the phrenic and intercostal nerves are paralyzed, and death takes place from suffocation. The attempt at respiration, however, still continues in these cases, showing itself by ineffectual inspiratory movements of the mouth and nostrils. Finally, if the medulla itself be broken up at the situation of the

respiratory centre, both the power and the stimulus to breathe are at once taken away. No attempt is made at inspiration and there is no appearance of suffering. The animal dies by want of aeration of the blood, which leads after some moments to arrest of the circulation.

An irregularity in the movements of respiration is accordingly one of the most threatening symptoms in affections of the brain. A suspension of the intellectual powers does not necessarily indicate immediate danger to life. Even sensation and volition may be impaired without direct injury to the organic functions. Cerebral apoplexy at the surface of the hemispheres, in the lateral ventricles, or in the cerebral ganglia, is seldom immediately fatal, however extensive may be the injury of the parts. But when occurring in the substance of the medulla oblongata or its immediate neighborhood, it produces death *instantaneously* by the same mechanism as where this part is intentionally destroyed by experiment in the lower animals. When the medulla is beginning to be implicated, in man, by a progressive disease or by gradual failure of the nervous functions, the respiratory movements first affected are those of the nostrils and lips, while those of the chest and abdomen go on for a time as usual. The cheeks are drawn in with every inspiration and puffed out with every expiration, the nostrils sometimes participating in these abnormal movements. A still more threatening symptom, and one which frequently precedes death, is an irregular and hesitating respiration, sometimes noticeable even before the remaining cerebral functions are seriously impaired. These phenomena depend on the connection between respiration and the reflex action of the medulla oblongata.

The process of *deglutition* is also accomplished under the control of the medulla. Mastication of the food by the movements of the jaws, and its transfer by the tongue to the entrance of the fauces, are voluntary actions which may be continued or arrested at will. But when the food has passed from the mouth into the pharynx, the act of deglutition, by which it is carried down into the stomach, is reflex and involuntary in character. Once commenced, it cannot be arrested by the influence of the will, as it consists of a series of muscular contractions following each other in regular and undeviating succession. These contractions receive their impulse from the medulla oblongata. In the experiments of Flourens and Longet, fowls and pigeons, after removal of the cerebral hemispheres, never picked up their food spontaneously, nor ever swallowed it when placed in the mouth at the end of the beak; but if carried backward and placed in the commencement of the pharynx, it was at once embraced by the muscular walls of this organ, and carried into the stomach by a continuous movement of deglutition. This includes, not only the associated contraction of the walls of the pharynx and œsophagus, but also the stoppage of respiration and the closure of the glottis, by which the food is prevented from passing into the larynx. According to Vulpian, after all parts of the brain have been removed, in cats or guinea pigs, excepting the medulla, swallowing may still be

accomplished by reflex action; but it becomes impossible as soon as this part is removed or seriously injured. The muscular combinations necessary to deglutition cannot take place, except under the influence of the medulla as a nervous centre.

This action may consequently be performed, in man, after all sensibility and voluntary power have disappeared. In cases of compression of the brain from injury or disease, when the individual is in a state of complete unconsciousness, and even when the respiration is diminished in frequency, solid or liquid food, if carried into the upper part of the pharynx, may be successfully swallowed by the ordinary movements of deglutition. When this process is no longer possible, or is accompanied by choking or regurgitation, it indicates that the medulla has become seriously affected, and that death is probably near at hand.

The medulla is furthermore connected with the act of *phonation*. The production of a vocal sound is usually the result of a voluntary impulse derived from the operation of the cerebral hemispheres. It is sometimes also a purely emotional act, originating in the excitement of the tuber annulare, and without any reasonable or intelligent motive. But in these cases its production is a secondary result, requiring the co-operation of other nervous elements, and its immediate centre is located in the medulla. This is shown by the fact that a cry may still be produced when the upper parts of the encephalon have been destroyed or removed, and when an irritation is applied to the medulla alone. If a stilet be introduced into the cranium of a frog, the cerebral hemispheres may be broken up without producing any excitement of the vocal organs; but when the instrument touches the medulla, its contact is often followed by a distinct and spasmodic cry. Vulpian has shown that a similar effect may be produced in mammalians, after removal of the whole encephalon excepting the medulla, by a reflex action. A cry is produced each time the integument of the foot is pinched by the blades of a forceps. This sound, however, gives no indication of consciousness or sensibility on the part of the animal. It is short, abrupt, and momentary in duration, and is repeated only when the irritation is again applied to the external parts. It is a purely mechanical effect of the tension of the vocal cords and the sudden expulsion of air through the rima glottidis. After the destruction of the medulla, on the other hand, no vocal sound can be produced, and the same irritation of the integument is then followed only by the ordinary spasmodic movement of the limbs, dependent on the reflex action of the spinal cord.

In the exercise of the voice, therefore, the preliminary actions of intelligence, volition, or emotional excitement require the co-operation of the cerebrum and the tuber annulare; but the immediate mechanism by which a vocal sound is produced in the larynx has its nervous centre in the medulla oblongata.

This part of the brain, with the adjoining part of the tuber annulare, is also the direct source of the movements of *articulation*. It is the gray substance of this region that gives origin to the hypoglossal and

facial nerves which animate the muscles of the tongue and lips, as well as the motor fibres which regulate the condition of the rima glottidis. Disease or injury in this situation, sufficient to impair the action of these nerves, consequently makes articulation difficult or impossible, by paralyzing the muscles upon which it is dependent. This affection is quite distinct from "aphasia," which is of cerebral origin and consists in a loss or deterioration of mental faculties alone, the external mechanism of speech being unaffected and the muscles of the tongue and lips retaining their power of movement in any direction. When the difficulty is seated in the medulla, on the other hand, the muscular paralysis is very evident, and is distinguished by being more or less confined to those groups of muscles which are concerned in articulation and phonation.

Such an affection is that first described by Duchenne and now generally recognized under the name of *glosso-labio-laryngeal paralysis.*[1] It is a paralysis due to chronic degeneration of gray nervous tissue in the medulla oblongata, which affects the motor nerves of the tongue, the face, the hanging palate, and the larynx. The first difficulty is generally noticeable in the movements of the tongue, which cannot be applied accurately to the upper teeth or to the roof of the mouth; and the lingual and dental consonants are therefore pronounced imperfectly or not at all. The lips are next affected, so that they cannot be brought in contact with each other, and B and P are pronounced like V or F. As the debility of the orbicularis oris increases, the lips cannot even be partially approximated and the vowels O and U are no longer sounded; and by the continued exaggeration of these difficulties the patient's speech becomes at last unintelligible. Deglutition is also affected, and attempts at swallowing are liable to cause choking, from the imperfect protection of the rima glottidis. Phonation becomes impaired from debility of the laryngeal muscles, and in advanced cases no vocal sound can be produced. The disease is uniformly progressive, and terminates life usually by affecting the movements of respiration.

The medulla oblongata is accordingly the seat of reflex actions which are directly or indirectly connected with the immediate preservation of life, since it maintains the movements by which air and food are introduced into the interior of the body. It also presides over the immediate muscular combinations concerned in the production of the voice and articulation, and by this means establishes an intelligible communication with the external world.

[1] Hammond, Diseases of the Nervous System. New York, 1871, p. 676.

CHAPTER VI.

THE CRANIAL NERVES.

Of the twelve pairs of nerves which take their origin from the brain, the greater number present distinct analogies, both anatomical and physiological, with the spinal nerves. All those which are distributed to the integument and mucous membranes, or to the superficial and deep muscles of the head and face, correspond in all important characters with the sensitive and motor nerves formed from the anterior and posterior spinal nerve roots. Three of them, however, show no resemblance, either in their anatomical distribution or their physiological properties, with the rest. They are the so-called olfactory, optic, and auditory nerves. After leaving their points of origin in the brain, they are distributed neither to muscles nor to the integument or mucous membranes; but terminate in nervous expansions of special form and structure, in which the gray substance or collections of nerve cells reappear as prominent elements of the tissue. During their passage through the cavity of the cranium, these nerves are neither sensitive nor excitable in the ordinary sense of the word. Their irritation causes no tactile or painful sensation, nor any direct muscular contraction; and their section produces no paralysis of the voluntary muscles, nor any loss of general sensibility in the neighboring parts. They are to be considered rather in the light of tracts or commissures than of ordinary nerves, and their physiological properties are those connected with the operation of the special senses alone.

The remaining cranial nerves, on the other hand, are similar, both in structure, arrangement and function, to those in other parts of the cerebro-spinal system. Some of them, like the oculo-motorius, the patheticus, and the facial, are plainly motor in character, are distributed to muscles, produce convulsive motion on being irritated, and, when injured or divided, leave the corresponding parts in a state of paralysis. Others, such as the trigeminus, the glosso-pharyngeal, and the pneumogastric, are sensitive nerves, possessing either an acute tactile sensibility, like the trigeminus, or one of a more obscure and special nature adapted for the production of involuntary reflex actions, like the glosso-pharyngeal and pneumogastric. Like the posterior roots of the spinal nerves, these are also provided with a ganglion situated at a short distance from their points of emergence at the base of the brain; and they are distributed either to the integument or mucous membranes or to both.

The analogy in anatomical arrangement between the spinal and cranial

nerves is in some instances very marked. The fifth pair or trigeminus emerges from the tuber annulare in two distinct bundles or roots, of which one is sensitive, the other motor; the sensitive root presenting soon afterward a well developed ganglion, with which the fibres of the motor root do not mingle. This nerve beyond the ganglion, therefore, contains both motor and sensitive fibres, and is distributed both to muscles and to the integument. In a similar manner the glosso-pharyngeal nerve is joined, beyond its ganglion, by motor fibres from the facial; and the pneumogastric receives abundant communications from the spinal accessory and other motor nerves. Both the sensibility and motion therefore of the parts to which they are distributed are provided for, in a manner not essentially different, by both the cranial and spinal nerves.

The other points, both of difference and analogy, in the cranial nerves, relate to their origin and distribution. Their apparent origin, that is, the point at which they become detached from the surface of the brain, is not their real origin; but in every case their fibres can be traced from this point inward, between other longitudinal or transverse tracts of white substance, until they reach a mass of gray matter, often placed at a considerable distance and in quite a different locality from their apparen origin. All the cranial nerves, excepting the olfactory and the optic, are thus found to originate from a mass of gray substance upon and beneath the floor of the fourth ventricle, and extending forward to surround the aqueduct of Sylvius. This layer of gray substance is a continuation of that in the spinal cord; but while in the cord it has the form of a central mass with lateral anterior and posterior horns, in the medulla oblongata it takes the shape of a lamina occupying only the posterior part of the cerebro-spinal axis. In its various divisions and expansions, which are rarely, if ever, completely discontinuous from each other, it forms the so-called "nuclei" of the cranial nerves.

In their distribution, these nerves present also certain anatomical features which are more apparent than real in their importance. The oculomotorius, patheticus, and abducens emerge from the substance of the brain at very different points, and, running forward through the cranial cavity in the form of separate cords, are enumerated as three distinct nerves. But they all originate from the layer of gray substance already mentioned, two of them, the oculomotorius and the patheticus, in close proximity to each other; they all pass out of the cranium, into the orbital cavity, by the sphenoidal fissure; and they are all distributed to the group of muscles moving the eyeball. In a physiological point of view, therefore, they are branches of a single nerve, rather than three separate trunks. Even when two or more nerves emerge from the cranium by different foramina, like the three divisions of the trigeminus, they are nevertheless, properly speaking, parts of the same nerve, if they have similar physiological properties and are distributed to the muscles or integument of the same regions. It is the ultimate distribution of a nerve, and not its course through the bones of the skull, that determines

its physiological character and position. The details of branching and division of the cranial nerves vary in different species of animals, or even to some extent in the same individual on the two opposite sides of the body, but their physiological characters remain the same. Thus in the bull-frog, as shown by Wyman,[1] both the facial nerve and the abducens, instead of existing as distinct trunks, are given off as branches from the fifth pair; and in most of the quadrupeds, the terminal frontal branches of the ophthalmic division of the trigeminus are wanting, or reduced to trifling dimensions, in accordance with the absence of sensibility in the skin of the forehead and vertex.

The cranial nerves may, therefore, be conveniently arranged in pairs according to their distribution and functions, rather than the incidental peculiarities of their course or subdivision. The olfactory, optic, and auditory nerves thus form a group by themselves of a specific character; while the remainder consist of the motor and sensitive nerves, supplying the muscular apparatus and the integument or mucous membrane of different regions.

CRANIAL NERVES.

Nerves of Special Sense.

1. Olfactory. 2. Optic. 3. Auditory.

	Motor nerves.	Sensitive nerves.	Distributed to the
1st PAIR.	Oculomotorius Patheticus Abducens Facial Small root of 5th pair	Trigeminus.	Upper, middle, and lower facial regions.
2d PAIR.	Hypoglossal	Glosso-pharyngeal.	Tongue and pharynx.
3d PAIR.	Spinal accessory	Pneumogastric.	Passages of respiration and deglutition.

This division of the nerves, though based on their physiological characters and distribution, is not absolutely perfect in all particulars. For while the hypoglossal nerve supplies the muscles of the tongue alone, its associate, the gloss-pharyngeal, sends a part of its sensitive fibres to the tongue and a part to the pharynx; and while the trigeminal nerve is mainly distributed to the external parts of the face, one of its deeper branches, the lingual, is distributed to the tongue. Notwithstanding, however, these irregularities, such an arrangement of the cranial nerves is substantially correct, and may serve as a useful guide in the study of their functions.

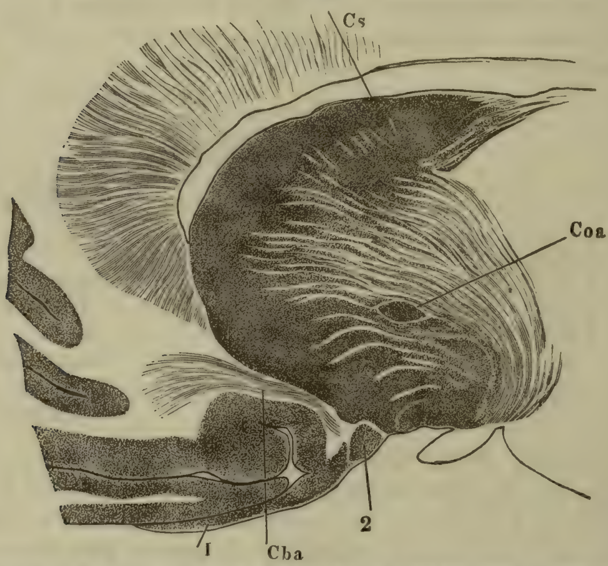
First Pair. The Olfactory Nerves.

What is called in man the "olfactory nerve," is a three-cornered prismatic tract, composed of both gray and white substance, running forward in a longitudinal groove upon the inferior surface of the anterior cerebral

[1] Nervous System of Rana pipiens; published by the Smithsonian Institution, Washington, 1853.

lobe, near the median line, and terminating anteriorly in a flattened ovoid mass of gray substance, the "olfactory bulb." The olfactory bulb rests upon the cribriform plate of the ethmoid bone, and gives off, through the perforations in this bone, the true nervous filaments supplying the olfactory membrane in the nasal passages. The prismatic tract which connects the olfactory bulb with the rest of the brain is in reality, according to both Henle and Meynert, a prolongation of one of the cerebral convolutions. It originates in a rounded eminence called the "olfactory tubercle," situated at the back part and under surface of the anterior cerebral lobe, just inside the island of Reil, with which it is connected. It consists, like the other cerebral convolutions, of gray substance containing pyramidal cells. Its peculiarity, as shown by Henle, consists in the fact that bundles of nerve fibres from the interior

Fig. 169.



LONGITUDINAL SECTION OF THE CEREBRAL HEMISPHERE, through the situation of the olfactory tubercle and part of the olfactory nerve.—1. Olfactory nerve. 2. Olfactory tubercle. Cs. Corpus striatum. Coa. Anterior cerebral commissure. Cba. Anterior commissure of the base of the brain. Magnified once and one half. (Henle.)

pass through its cortical layer of gray matter, and appear upon its surface as more or less distinct striations of white substance. It is these white striations which have been designated as the olfactory "roots," and which give to the tract terminating in the bulb the external appearance of a nerve. They are derived from the white substance of the cerebral hemispheres, and continue forward to the gray matter of the olfactory bulb. A communication is established between the olfactory nerves of the two opposite sides through the internal white substance of the olfactory tubercles. According to Vulpian, there is also a more direct communication, visible in the dog, the sheep, and the

rabbit, formed by one of the so-called olfactory nerve roots, which turns inward and crosses the median line, in company with the fibres of the anterior cerebral commissure.

Physiological Properties of the Olfactory Nerve.—The olfactory nerve thus formed is a tract of communication between the central parts of the brain and the olfactory bulb. Its physiological connection with the sense of smell is indicated by, 1st, its anatomical relations; 2d, its comparative development in different species of animals; and 3d, the results of its injury or disease.

I. The only anatomical connection of the olfactory nerve, at its anterior extremity, is with the olfactory bulb; and the nerve fibres given off from this part are distributed only to the olfactory region of the nasal passages. In this region ordinary sensibility is but slightly developed, while the parts are highly endowed with the sense of smell.

II. In such of the lower animals as possess a more acute sense of smell than man, like the dog, the cat, the sheep, and other quadrupeds, the olfactory bulbs are increased in proportion, forming prominent masses at the anterior extremity of the hemispheres; while the parts representing the olfactory nerves are of so large a size that they are generally designated by the name of the "olfactory lobes." They also contain a central tubular cavity, which is a prolongation from that of the lateral ventricles. There is accordingly a direct correspondence between their development and that of the special sense with which they are connected.

III. A considerable number of cases are quoted by Longet in which congenital absence of the olfactory nerves, in man, was accompanied by congenital incapacity to distinguish odors; and others in which a loss of the sense of smell was also observed after morbid affections causing compression or destruction of these nerves.

According to the experiments of Magendie upon dogs,[1] the olfactory nerves are not sensitive to mechanical irritation, since their compression, puncture, or laceration in various directions, in the living animal, causes no perceptible indications of sensibility.

Finally, experimental division or destruction of these nerves in dogs abolishes, so far as observation can show, the power of discriminating odors; although it leaves the nasal mucous membrane sensitive to the irritation of pungent or caustic vapors. In the experiments of Magendie, a dog, after destruction of both olfactory nerves, would disentangle a package containing meat when openly presented to him; but he did not find it, when placed near by without his knowledge. The same result was obtained by Vulpian[2] in operating upon hunting dogs. These animals, after recovering from the immediate effects of the operation, were kept fasting from 36 to 48 hours, and then introduced

[1] Journal de Physiologie Expérimentale et Pathologique. Paris, 1825, tome iv. p. 170.

[2] Leçons sur la Physiologie du Système Nerveux. Paris, 1866, p. 882.

into an apartment where a piece of cooked meat was concealed; but they were never able to discover it by its odor, when the division of the nerves had been complete. Notwithstanding, therefore, the comparative difficulty of experimenting upon so obscure a function as that of smell, there is no doubt that the olfactory nerves and bulbs are really the internal organs of the olfactory sense, and that they are disconnected both with ordinary sensibility and the power of motion.

Second Pair. The Optic Nerves.

The optic nerves take their first origin from the anterior pair of the *tubercula quadrigemina*, two small rounded prominences, on each side of the median line, situated just behind the posterior extremity of the optic thalami. They consist essentially of swellings of the gray substance which surrounds at this situation the aqueduct of Sylvius, and which is consequently continuous with that extending forward from the floor of the fourth ventricle. Their surface is covered by a layer of white substance from 1.5 to 4 millimetres in thickness, consisting of nerve fibres which have mainly a transverse direction. Their gray substance contains nerve cells, some of which are small and rounded, while others, especially in the anterior pair, are of larger size and provided with branched prolongations. According to Henle, the fibres of origin of the optic nerve pass from these bodies outward and downward to the *corpus geniculatum internum*, an ovoidal prominence of gray matter attached to the posterior border of the optic thalamus. They cover the surface of this body in a thin superficial layer, and continue their course, winding round the lateral surface of the crus cerebri; where they are joined at an acute angle by a second bundle of fibres, coming from the *corpus geniculatum externum*, a gray eminence similar to the last, lying in contact with the under part of the optic thalamus, but isolated from its gray matter by a thin investing layer of white substance. These two bundles of fibres, coming, one from the anterior tubercula quadrigemina and the corpus geniculatum internum, the other from the corpus geniculatum externum, form in man the two roots of the optic nerve; and the collections of gray matter contained in these bodies are regarded as its "nuclei," or the nervous centres with which it is in anatomical communication. It also receives some fibres from the substance of the optic thalamus itself.

The fibres derived from these sources form a flattened band which continues its course in a spiral direction, winding round the crus cerebri to the base of the brain; it thence runs forward and inward until the two, from the right and left sides, meet upon the median line in the so-called "chiasma," or decussation. From this they again diverge outward and forward, leave the cavity of the cranium by the optic foramina, and, joining the eyeballs, terminate in the nervous expansion of the retina. That portion of the optic nerves situated behind the decussation is sometimes designated by the special name of the "optic tract."

Real Origin of the Optic Nerves.—The fibres of the optic nerves, in man, as shown by the above description, cannot all be distinctly traced in a direct manner to the tubercula quadrigemina; but those of one root are evidently connected with the corpus geniculatum externum, while those of the other pass to the corpus geniculatum internum, and through the intervention of that body alone reach the anterior quadrigeminal tubercule. And yet the data derived from comparative anatomy, as well as the results of experiments upon the tubercula quadrigemina, show that in the lower animals these bodies are the real sources of the optic nerves. In all the mammalian quadrupeds the optic nerves are readily seen to have their direct origin in the tubercula quadrigemina. In the birds, reptiles, and fish these bodies are divided only into two symmetrical prominences by a shallow, longitudinal, median furrow; and in these classes, accordingly, they are called the "tubercula bigemina." But they are of comparatively larger size than in the mammalians, and give origin still more distinctly to the optic nerves. Furthermore, their destruction, as shown by the united testimony of all observers, produces at once a loss of sight, although the remaining parts of the brain be left uninjured; while it is certain, on the other hand, that both the hemispheres and the optic thalami may be removed without destroying sensibility to light. Even in man, according to the observations of Vulpian, the optic thalami may be the seat of extensive lesions, from hemorrhage or softening, without any sensible disturbance of the power of vision.

The apparent variation in man from the general type, in respect to the origin of the optic nerves, is most readily explained by the variation in the comparative size of the tubercula quadrigemina and the optic thalami. In the inferior vertebrate animals, namely, fish and reptiles, the tubercula quadrigemina or their representatives are very large, and the optic thalami are either wanting or so slightly developed as to make their significance uncertain. In birds the optic thalami are present, but are still inferior in size to the tubercula bigemina. In mammalians they increase in size in the ascending series, but the tubercula quadrigemina are still, in such animals as the dog and cat, comparatively conspicuous, and, throughout this class, consist of four tubercles instead of two. In man the optic thalami are very much larger than the tubercula quadrigemina, which are reduced altogether to a secondary grade. The corpora geniculata probably represent in man portions of gray substance included, in the lower animals, in the tubercula quadrigemina or bigemina; but which in the human brain are crowded outward and backward by the increased development of the optic thalami, and therefore appear as appendages of these bodies.

Physiological Properties of the Optic Nerves.—The optic nerves, like the olfactory, are nerves of special sense, and may be regarded as tracts of fibres connecting the gray matter of the cerebrum with the retinal expansion of the globe of the eye. They are destitute of sensibility to tactile or painful impressions, and convey from without inward

only the impression produced upon the retina by luminous rays. In the central parts of the brain with which they are connected, this impression becomes the sensation of light; and the optic nerves are therefore the channels for the sense of vision. Magendie found that in quadrupeds both the retina and the optic nerves throughout their length were insensible to mechanical irritation; and, in man, that touching the retina with the point of a cataract needle excited no perceptible sensation. It has also been remarked, in cases of extirpation of the eyeball, that the section of the optic nerve is not a painful part of the operation; and, according to the observations of Longet upon animals, these nerves may be pinched, pricked, cauterized, divided, or injured in various ways without producing any signs of pain.

On the other hand, division of these nerves at once produces a state of blindness. The impressions received by the retina are no longer transmitted to the central organ, and the animal becomes insensible to light, without losing any of his ordinary tactile sensibility or power of voluntary motion.

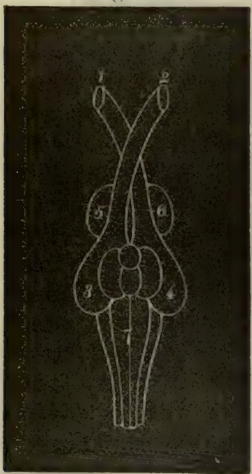
Beside their immediate function in the perception of light, the optic nerves are also channels for a special reflex action, connected with the mechanism of vision; namely, that of the *contractile movements of the iris.* By these movements the orifice of the pupil enlarges or diminishes according to the intensity of the light to which the eye is exposed. On first entering a dark room everything is nearly invisible; but gradually, as the pupil dilates and as more light is admitted, objects show themselves with greater distinctness, and at last we can see tolerably well where it was at first almost impossible to perceive a single object. On the other hand, when the eye is exposed to a brilliant light, the pupil contracts and shuts out so much of it as would be injurious to the retina.

These movements, by which the quantity of light admitted to the eye is regulated to suit the sensibility of the retina, are involuntary in character, but are due to impressions conveyed inward by the optic nerve. On the division of these nerves, or the destruction of the tubercula quadrigemina, not only is the perception of light abolished, but the pupil remains immovable, whatever may be the intensity of the light to which it is exposed. In the production of this reflex act, the impression, which is first received upon the retina, passes inward through the fibres of the optic nerve to the tubercula quadrigemina. Its transformation into a motor impulse is either accomplished in these bodies, or is commenced in them and completed by transmission to the gray matter at the origin of the oculomotorius nerves. Thus both the optic nerves and the tubercula quadrigemina are essential to the movements of the pupil under the influence of light. The proof that this action is of a reflex nature is afforded by the results of dividing and irritating the optic nerves. After section of the nerve, according to the experiments of Herbert Mayo and Longet, upon pigeons, dogs, and rabbits, irritation of its *peripheral* end, that is, the portion still connected with the eyeball, produces no effect upon the pupil; but irritation of its *central* portion, which is connected

only with the brain, readily causes a movement of contraction. On the other hand, division of the oculomotorius nerve, which paralyzes the iris, puts an end to the movements of the pupil, although the eye may be otherwise uninjured and the perception of light unimpaired.

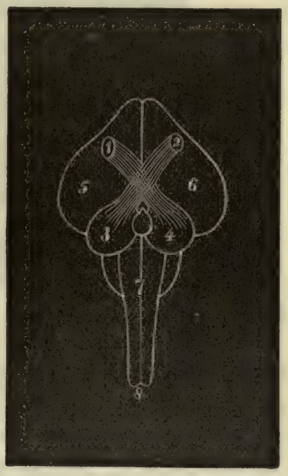
Decussation of the Optic Nerves.—The decussation of these nerves forms one of their most prominent anatomical features, being in all cases readily visible on superficial examination, while in many classes of the lower animals and in man it presents, on closer inspection, certain marked varieties of detail. In fish, as a general rule (Fig. 170), the two optic nerves cross each other's path from side to side at different levels, without any admixture or even contact of their fibres; that from the right side of the brain passing independently to the left eye, and that from the left side of the brain to the right eye. In the herring, according to Wagner, the optic nerve of the right eye perforates that of the left, passing bodily through it by a distinct slit, without forming a chiasma. In the sharks and rays, which have a higher general grade of organization than other fish, the fibres of the two nerves cross each other in separate fasciculi.

Fig. 170.



Inferior Surface of the Brain of the Cod.—1. Optic nerve of right eye. 2. Optic nerve of left eye. 3. Right optic tubercle. 4. Left optic tubercle. 5, 6. Cerebral hemispheres. 7. Medulla oblongata.

Fig. 171.



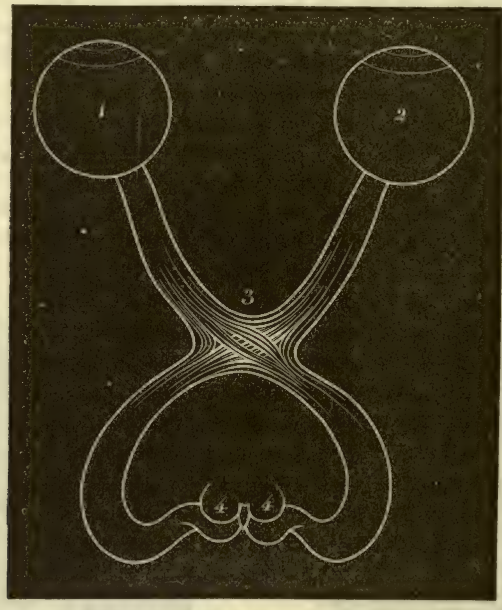
Inferior Surface of the Brain of Fowl.—1. Optic nerve of right eye. 2. Optic nerve of left eye. 3. Right optic tubercle. 4. Left optic tubercle. 5, 6. Cerebral hemispheres. 7. Medulla oblongata.

In birds the two optic nerves appear externally to be united at their point of crossing (Fig. 171), but dissection shows that the decussation of their fibres is complete. Those coming from the left side pass, in the form of slender bundles, altogether over to the right, and those from the right side pass in the same manner over to the left; so that in this class each optic tubercle is connected exclusively with the eye of the opposite side.

In man the decussation is more complicated, and is arranged in such

a manner as to form a connection at the same time between the two opposite sides, and between the eye and the quadrigeminal tubercle on the same side. Here also the apparent majority of the fibres cross each other completely from side to side, though intermingled at the chiasma in such slender bundles that they are distinguishable only by microscopic examination. But at each side of the chiasma there is also a layer of fibres, which, according to Henle, hardly exceeds one-twentieth of a

Fig. 172.



COURSE OF THE OPTIC NERVES IN MAN.—1, 2. Right and left eyeballs. 3. Decussation of the optic nerves. 4, 4. Tubercula quadrigemina.

millimetre in thickness, passing continuously along its outer border and thence running forward with the optic nerve to the eye of the same side. These fibres, like those of the white substance in general, do not keep the same horizontal level, but follow a more or less spiral course, winding successively outward, downward, and inward, from the upper surface of the chiasma to reach the under surface of the optic nerve in front. It is not known in what special parts of the retina the two sets of fibres on each side, namely, the decussating and the direct, find their termination.

At the anterior angle of the chiasma there are also fibres which pass from side to side in a curved direction, running symmetrically across from one optic nerve to the other, and forming a transverse commissural band between the retinæ of the two eyes; and finally at the posterior angle of the chiasma there are similar transverse commissural fibres, which pass forward on each side with the corresponding optic tract, cross the median line at the chiasma, and return backward with the optic tract of the opposite side. Thus there is effected a fourfold connection

between the two eyes and their nervous centres, namely, 1st, that between each nervous centre and the opposite eye; 2d, that between each nervous centre and the corresponding eye; 3d, that between the two eyes by the anterior transverse commissure; and 4th, that between the two nervous centres by the posterior transverse commissure.

The physiological significance of this compound decussation is not clearly understood. When compared as it presents itself in different classes of animals, it appears to be connected with the degree of divergence or parallelism between the visual axes of the two eyes. Thus in fish, where the eyes are so placed on opposite sides of the head that their axes cannot be brought into parallelism with each other, the optic nerves cross from side to side as distinct cords going to the opposite eyes. In birds, where the eyes have nearly the same relative position as in fish, the decussation is also complete, though less evident externally. In quadrupeds as a class, the eyes are set more obliquely forward, while in man they are situated completely at the front, so that their visual axes are both directed forward, and parallel with each other, or may even converge, and the two eyes can thus be brought to bear at the same time upon near objects. The quadruple communication which exists in man is, therefore, usually regarded as connected in some way with the capacity for distinct and single vision with the simultaneous use of both eyes. Cases, however, like that related by Vesalius,[1] in which the decussation was wanting, each optic nerve going independently to the eye of its own side, without any noticeable defect of vision, show that such a communication is not directly or absolutely necessary, even in man, to distinct vision of single objects. It more probably serves in an indirect manner, by reflex action, to facilitate the harmonious muscular control of the two eyeballs, by which the corresponding parts of the retina on the two sides receive the visual rays coming from a single object.

Crossed Action of the Optic Nerves.—The results of observation show that the action of the optic nerves, as channels for the sense of sight, is mainly a crossed action. The experiments of Flourens, Longet, and Vulpian coincide in this respect; and in regard to birds the fact is easily established. If in the pigeon, as we have frequently observed, the right optic tubercle alone be removed, when the bird has recovered from the immediate effects of the wound, the sight is to all appearance completely lost in the eye of the opposite side, but remains unimpaired in the eye of the same side. After such an operation an instrument may be carefully brought in close proximity to the left eye, without producing any sign of its perception; but the instant it is moved a little in front, so as to come within the range of the right eye, the animal starts backward to avoid it. Flourens obtained similar results in the dog and rat, leading to the conclusion, which agrees with that of Longet, that in quadrupeds also visual impressions are transmitted by the optic

[1] De Humani Corporis Fabrica. Liber iv. cap. iv.

nerves entirely in a crossed direction. There is no question that these animals after destruction of the tubercula quadrigemina on one side are mainly blinded in the opposite eye, since they use exclusively the eye of the wounded side to guide them in their motions.

In man, the partial blindness of both eyes, sometimes observed in cases of hemiplegia, makes it probable that the transmission of sight takes place by both the crossed and direct fibres of the optic tracts.

The reflex influence which causes contraction of the pupil is also transmitted, in the lower animals, in a crossed direction; that is, the stimulus of light falling upon the retina of one eye passes to the optic tubercle of the opposite side. But here, owing to the transverse connections between the central parts of the brain, the stimulus becomes duplicated, and contractions are produced in the pupils of both eyes simultaneously. This is because, although the sensitive impression is conveyed inward to the nervous centres by one optic nerve only, when transformed into a motor impulse it may be sent outward by both oculomotorius nerves at the same time. Consequently if, in a pigeon, one eye be blinded by removal of the opposite optic tubercle, both pupils will still contract under the stimulus of light applied to the sound eye. In examining one eye, therefore, either in animals or in man, to ascertain whether or not its retina be sensitive to light, the opposite eye should always be covered, in order to prevent its exciting a movement by reflex action.

Third Pair. The Oculomotorius.

The oculomotorius nerve, so called because it supplies four out of six of the muscles moving the eyeball, originates from a collection of gray substance situated next the median line, beneath the tubercula quadrigemina and the aqueduct of Sylvius. As this group of nerve cells is continuous with that which gives origin to the fourth nerve or patheticus, it is sometimes designated as the *common nucleus of the oculomotorius and patheticus nerves.* From this nucleus the fibres of the oculomotorius nerve pass downward and forward, through the substance of the crus cerebri, until they emerge, in the form of several flattened bundles, from its inner border, a little in front of the anterior edge of the pons Varolii. From this point, the apparent origin of the nerve, its fibres unite into a rounded cord, which runs forward and outward, to penetrate the cavity of the orbit by the sphenoidal fissure. During its transit along the walls of the cavernous sinus, it receives one or two fine twigs of sensitive fibres from the trigeminus nerve. In entering the orbit, it divides into several branches, and supplies the superior, inferior, and internal straight muscles of the eyeball, the inferior oblique, and the levator palpebræ superioris. The oculomotorius is accordingly concerned both in the vertical and lateral movements of the eyeball, and in those of rotation; while of the two other muscular nerves of this organ, the abducens and patheticus, one is connected only with the movement of lateral abduction, the other only with that of rotation.

Decussation of the Oculomotorius Nerve.—According to the observations of Meynert, a decussation takes place between the oculomotorius nucleus and the opposite side of the brain, by means of fibres emerging from the raphe upon the median line, near which the nucleus is situated. These fibres come originally from the corpus striatum, thence running backward along the inner border of the crura cerebri, into the longitudinal lamina forming the raphe between them. Underneath the aqueduct of Sylvius they decussate with each other at acute angles, those from the right corpus striatum passing to the nucleus of the left side, and *vice versâ.* Each oculomotorius nerve is therefore in connection with the opposite side of the brain, not by means of its own fibres, but through the intervention of its nucleus and the fibres which pass thence, through the raphe, toward the opposite corpus striatum.

Physiological Properties of the Oculomotorius Nerve.—The oculomotorius is in itself an exclusively motor nerve, and has been found by Longet, when examined in the living animal, near its point of emergence from the crus cerebri, to be insensible to mechanical irritation; but at some distance farther forward, after receiving its branches of communication from the fifth pair, it exhibits a certain degree of sensibility. Its excitability, on the contrary, is very manifest; and its irritation within the cranial cavity, even after it has been separated from its connection with the brain, causes convulsive action in the muscles of the eyeball.

The physiological function of this nerve is distinctly shown by the nature of the paralysis following its section either before or after its entrance into the orbit. These results are for the most part very simple and well marked, and are established by the uniform testimony of various observers. They consist of the paralysis of the five muscles to which the nerve is distributed, and induce, consequently—

1. *External strabismus*, from continued action of the external straight muscle of the eyeball, which is no longer controlled by that of the internal.

2. *General immobility of the eyeball*, owing to the abolition of its natural upward, downward, lateral, and rotatory movements. For although two of the muscles of the eyeball, namely, the external rectus and the superior oblique, remain unparalyzed; yet, as they are no longer antagonized by the remainder, they can only produce a permanent deviation of the eyeball, but no alternate movement in opposite directions. In most of the lower animals there is also an unusual prominence of the eyeball, owing to the relaxed condition of the muscles which serve for retraction.

3. *Drooping of the upper eyelid.* In the ordinary action of opening the eye, it is the upper eyelid alone which moves, being raised so as to uncover the cornea and pupil, by the contraction of the levator palpebræ superioris. As this muscle is animated by a nervous branch coming from the oculomotorius, it is paralyzed by section of this nerve at the same time with the muscles moving the eyeball. The consequence is

that the eye can no longer be opened to its full extent; although it can still be closed as usual by the action of the orbicularis oculi, which does not depend upon the oculomotorius, but is animated by branches derived from the seventh pair, or facial nerve. The superior eyelid therefore droops, resting by its own weight in such a position as to cover the upper portion of the cornea, and the greater part or even the whole of the pupil. In man this condition of the eyelid is known as *ptosis*, and is one of the consequences following paralysis of the oculomotorius nerve.

The influence of the oculomotorius upon the *contractile movements of the iris* is important, though less distinct and uniform in its action, as shown by experiment, than that exerted upon movements of the eyeball itself. The connection of the oculomotorius with the muscular apparatus of the iris is not a direct one, but takes place through the intervention of the ophthalmic ganglion, to which this nerve sends a communicating motor branch, and which in turn gives off the ciliary nerves destined for the iris. Some observers (Herbert Mayo, Longet) have found well-marked paralysis of the iris following division of the oculomotorius nerve, and enumerate, as consequences of this injury, a permanent dilatation and immobility of the pupil. In the experiments of Longet, which were performed on dogs, rabbits, and pigeons, irritation of the cephalic extremity of the optic nerve caused contraction of the pupil in both eyes; but after division of the oculomotorius nerve the effect was no longer produced upon the operated side. Bernard has also found that division of the oculomotorius is followed, in the rabbit, by dilatation of the pupil, and that in the operated eye the iris contracts only very slowly and imperfectly under the influence of light. It is not, however, completely paralyzed, since it may still move with considerable promptitude under the influence of painful impressions conveyed by the fifth pair. The action of the oculomotorius upon the pupil, therefore, is energetic and constant in the ordinary reflex movement of contraction under the stimulus of light; but it takes place through the ophthalmic ganglion, to which it communicates, in a certain degree, its motive power.

Fourth Pair. The Patheticus.

This nerve presents a variety of peculiarities, which have always, notwithstanding its minute size, attracted to it more or less special attention. It is distributed exclusively to the superior oblique muscle of the eyeball; its name having been derived from the mistaken idea that this muscle turned the eye upward and inward. The two oblique muscles, however, have been fully shown to cause in the eyeball a nearly simple movement of rotation about its longitudinal axis. They are antagonistic to each other; and by their contraction and relaxation, during movements of inclination of the head from side to side, they maintain the horizontal planes of the two eyeballs in the same position. If this parallelism were not preserved, objects would appear to stand in

different degrees of obliquity to the two eyes, producing uncertainty and double vision.

The apparent origin of the patheticus nerve is directly behind the tubercula quadrigemina, on the upper surface of the *valve of Vieussens*, a thin lamina of white substance, extending from this situation backward to the cerebellum, and thus covering in the anterior part of the fourth ventricle. The fibres of the nerve, however, can be traced from without inward in a transverse direction through the substance of the valve. According to Henle and Meynert, a great part of these fibres cross the median line, decussating with those coming in the opposite direction from the corresponding nerve on the other side; then, turning downward and forward, they reach a collection of gray matter seated just behind the nucleus of the oculomotorius nerve, and continuous with it anteriorly. According to Henle, a portion of the fibres also remain upon the same side of the median line, and terminate, without crossing, in this and another nucleus not far distant. The collection of gray matter just described is, however, regarded as the main nucleus or point of origin for the fibres of the patheticus nerve. This nucleus is situated beneath the aqueduct of Sylvius, near the median line, and at a situation corresponding with the anterior tubercula quadrigemina; while the point of exit of the nerve is above the aqueduct of Sylvius and behind the posterior tubercula quadrigemina. Its fibres, accordingly, after leaving the gray matter in which they originate, encircle the lateral walls of the aqueduct, running obliquely upward and backward, and then, curving inward, cross the median line to their point of emergence on the opposite side.

From this point the nerve passes forward, as a slender, rounded filament, not more than one millimetre in diameter, but containing, according to the estimate of Rosenthal, about 1100 ultimate nerve fibres. It passes along the upper wall of the cavernous sinus, where it lies in immediate proximity to the oculomotorius; and thence, entering the cavity of the orbit by the sphenoidal fissure, terminates in the substance of the superior oblique muscle of the eyeball.

The course of the fibres of the oculomotorius and patheticus, when compared with each other, shows a remarkable relation between two nerves which are apparently distinct. The fibres of both originate from adjacent portions of the same nucleus, situated in the thickness of the crus cerebri. Those of the oculomotorius pass downward and forward, to emerge from the inner free border of the crus, at the base of the brain; while those of the patheticus pass upward and backward, to emerge from the upper and posterior part of the cerebro-spinal axis, between the cerebrum and cerebellum. But the two nerves afterward pass side by side, in their passage toward the orbit, and are finally distributed to muscles which are associated in the accomplishment of the same movements.

Physiological Properties of the Patheticus Nerve.—The anatomical distribution of this nerve to a muscle which receives filaments from no

other source indicate in great measure its motor character, which is furthermore fully established by the results of observation. Both the experiments of Chauveau on the horse and rabbit, and those of Longet on the horse, ox, and dog, show that galvanization of this nerve in the interior of the cranium produces always contraction of the superior oblique muscle of the eyeball, with rotation of the eyeball on its longitudinal axis from without inward ; and in those of Longet there was also a perceptible deviation of the pupil outward. In cases quoted by Longet, in the human subject, attributed to paralysis of this nerve, there was incapacity of rotation of the eyeball on the affected side, and consequently double vision, the image perceived by the affected eye being oblique and inferior in regard to the other; but these disturbances of vision disappeared when the head was inclined toward the opposite side.

The patheticus is, accordingly, the motor nerve of the superior oblique muscle, and acts in harmony with the oculomotorius to preserve the horizontal plane of the eyeball.

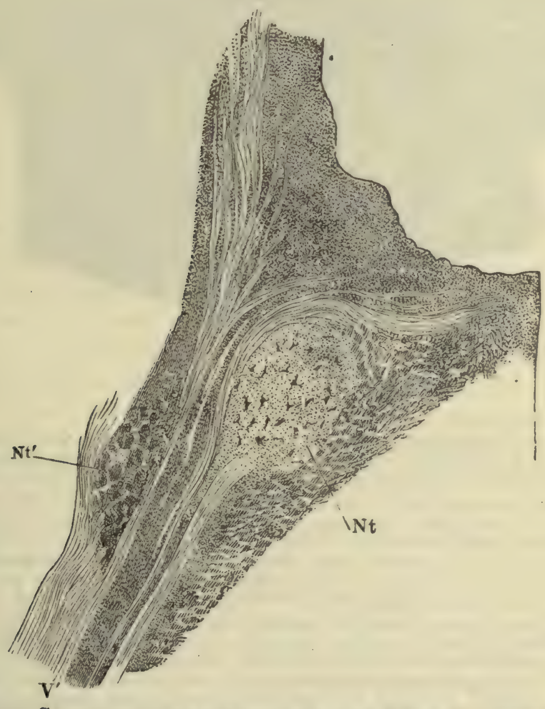
Fifth Pair. The Trigeminus.

The fifth pair occupies, in every respect, a prominent place among the cranial nerves. It is the great sensitive nerve of the face, being the only source of general sensibility for the integument and mucous membranes of this region; and, by communicating branches sent to the corresponding motor nerves, it also provides for the imperfect degree of sensibility belonging to the facial muscles. While in its main portion, however, it is thus pre-eminently a sensitive nerve, it also possesses motor fibres, derived from a distinct root, and distributed to muscles of a distinct group. Before emerging from the cranial cavity it separates into three main divisions, destined for the corresponding regions of the face; and its name, trigeminus, is derived from the fact that these three primary divisions of the nerve are nearly alike in size and importance.

The apparent origin of the fifth nerve is from the lateral portion of the pons Varolii, where its two roots emerge in close approximation to each other, but usually separated by a narrow band of the transverse fibres of the pons. The anterior or motor root is the smaller, being about two millimetres in diameter; the posterior or sensitive root is the larger, and having a diameter of about five millimetres. Both these roots may be traced, through the fibrous bundles of the pons Varolii, backward, upward, and inward toward the gray substance beneath the floor of the anterior part of the fourth ventricle. The two roots, which remain distinctly separated throughout most of their passage through the pons, join each other above and become closely entangled by the interweaving of their bundles; though their fibres may still be distinguished, on microscopic examination, by the generally larger size of those belonging to the motor root. They finally reach a collection of gray matter, the " nucleus of the fifth nerve," which is situated

next behind that of the oculomotorius and patheticus, but farther outward from the median line, occupying the extreme lateral part of the fourth ventricle, where its floor forms an angle with the roof. The fibres of the nerve terminate partly in or among the large, stellate, and dark-colored cells of the nucleus. According to Henle, a portion of them also pass through the nucleus, nearly to the surface of the floor of the ventricle, and thence inward to the raphe at the median line, where they cross to the opposite side; while another portion still, remaining upon the same side, pass upward with the superior peduncles of the cerebellum, and lose themselves in the substance of the tubercula quadrigemina. The fibres of the fifth nerve, accordingly, which terminate in the nucleus proper, form partly a direct, and partly a crossed connection between the external organs and the nervous centres.

Fig. 173.



Transverse Section of the Floor of the Fourth Ventricle, at the situation of the nucleus of the Trigeminus Nerve; Human brain.—Nt, Nt', median and lateral portions of the nucleus. V'. Fibres of the nerve root. Magnified 8 diameters. (Henle.)

After emerging from the pons Varolii, the two roots of the fifth nerve pass outward and forward in company with each other, the larger, posterior, or sensitive root being placed above, the smaller, anterior, or motor root underneath. On reaching the apex of the petrous portion of the temporal bone, a little outside and behind the posterior clinoid

processes of the sella turcica, the fibres of the sensitive root spread out into a comparatively loose network of inosculating bundles, and pass into and through the substance of the *Gasserian ganglion.* This ganglion forms a flattened, crescentic mass of gray matter, mingled with

Fig. 174.

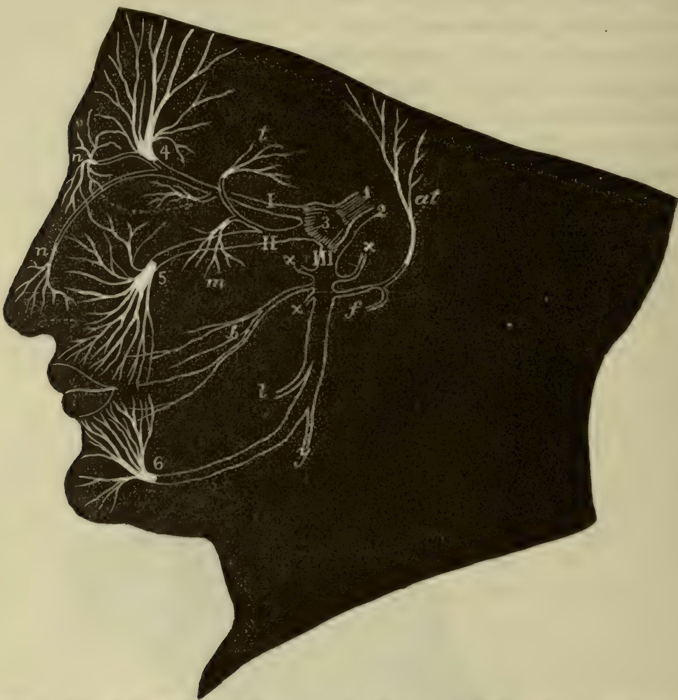


Diagram of the Fifth Nerve and its Distribution.—1. Sensitive root. 2. Motor root. 3. Gasserian ganglion. I. Ophthalmic division. II. Superior maxillary division. III. Inferior maxillary division. 4. Supra-orbital nerve, distributed to the skin of the forehead, inner angle of the eye, and root of the nose. 5. Infra-orbital nerve; to the skin of the lower eyelid, side of the nose, and skin and mucous membrane of the upper lip. 6. Mental nerve; to the integument of the chin and edge of the lower jaw, and skin and mucous membrane of the lower lip. *n, n.* External terminations of the nasal branch of the ophthalmic division, to the mucous membrane of the inner part of the eye and the nasal passages, and to the base, tip, and wing of the nose. *t.* Temporal branch of the superior maxillary division; to the skin of the temporal region. *m.* Malar branch of the superior maxillary division; to the skin of the cheek and neighboring parts. *b.* Buccinator branch of the inferior maxillary division; passing along the surface of the buccinator muscle, and distributed to the mucous membrane of the cheek, and to the mucous membrane and skin of the lips. *l.* Lingual nerve; to the mucous membrane of the anterior two-thirds of the tongue. *at.* Auriculo-temporal branch of the inferior maxillary division; to the skin of the anterior part of the external ear and adjacent temporal region. *x, x, x.* Muscular branches; to the temporal, masseter, and internal and external pterygoid muscles. *y.* Muscular branch; to the mylo-hyoid and anterior belly of the digastric muscles. *f.* Sensitive branch of communication to the facial nerve.

the fibres derived from the sensitive root. According to the observations of Kölliker, the fibres of the sensitive root simply pass through the gray matter of the ganglion, making no anatomical connection with its nerve cells; while the ganglion cells, which are mostly unipolar in

form, give off additional fibres in a peripheral direction. Thus the branches of the fifth nerve beyond the ganglion contain, beside the fibres derived from its sensitive root, others which have originated from the ganglion itself. The motor root passes underneath the ganglion as a distinct bundle, and neither gives to nor receives from it any nerve fibres. At the anterior or convex border of the Gasserian ganglion, the nerve separates into three nearly equal cylindrical bundles, namely, the first, or ophthalmic; the second, or superior maxillary; and the third, or inferior maxillary divisions of the fifth nerve.

The *ophthalmic division* passes forward through the sphenoidal fissure into the orbit of the eye, where it gives filaments to the ophthalmic ganglion and to the eyeball; a nasal branch which supplies the integument and mucous membrane of the inner part of the eye, the mucous membrane of the middle and inferior nasal passages, and the integument of the root, wing, and tip of the nose; and a branch to the lachrymal gland and the integument of the upper eyelid and adjacent region. It then emerges from the cavity of the orbit by the supra-orbital notch, and is distributed to the skin of the forehead and side of the head, as far back as the vertex.

The *superior maxillary division* passes out of the cranial cavity, by the foramen rotundum, at the base of the skull, into the spheno-maxillary fossa, where it gives a sensitive branch to the spheno-palatine ganglion of the sympathetic, thence into and through the longitudinal canal in the floor of the orbit, giving off a branch which runs upward and outward to terminate in the skin of the malar and temporal regions, and numerous descending branches, which supply the teeth, gums, and adjacent mucous membrane of the upper jaw, and, by a nasal filament, the mucous membrane of the bottom of the nasal passages. The nerve then emerges upon the face by the infra-orbital foramen, and is distributed in abundant diverging branches to the integument of the lower eyelid and the side of the nose, and to the skin and mucous membrane of the upper lip.

The *inferior maxillary division* leaves the anterior border of the Gasserian ganglion at a different angle from the two others, passing almost vertically downward through the foramen ovale. This division receives all the fibres of the motor nerve root, which become more or less intimately united to it during and after its passage through the base of the skull. While the two other divisions of the fifth nerve are therefore exclusively sensitive, the inferior maxillary division is a mixed nerve, containing both motor and sensitive fibres. Its sensitive portion, however, is still the most abundant, and all its motor branches are given off a short distance below its point of exit from the skull.

After emerging from the foramen ovale, this division of the fifth pair supplies one or two filaments to the otic ganglion of the sympathetic, which is situated near its inner surface, and passes downward toward the inferior dental canal; sending off, in the mean time, two sensitive branches, namely, 1st, the *buccinator* branch (*b*), destined for the mucous

membrane of the cheek, and the skin and mucous membrane of the lips; and 2d, the *auriculo-temporal* branch (*at*), which turns backward and upward behind the neck of the inferior maxilla, to be distributed to the integument of the anterior wall of the external auditory meatus, the anterior part of the external ear, and the adjacent temporal region. From this branch a twig of considerable size is given off (*f*), which turns forward to join the facial nerve, and communicates to its branches in front of this point a perceptible degree of sensibility.

Continuing its course, the nerve enters the dental canal of the inferior maxilla, through which it runs from behind forward, giving off filaments to the teeth and gums of the lower jaw. It then emerges at the mental foramen, and radiates, like the corresponding portion of the superior maxillary division, in diverging branches and ramifications, which terminate in the integument of the chin and edge of the under jaw, and in the skin and mucous membrane of the lower lip.

The remaining sensitive branch of this portion of the fifth is the *lingual nerve* (*l*), which separates from it before its entrance into the dental canal, sends filaments to the submaxillary gland, the sympathetic submaxillary ganglion, and the adjacent mucous membrane of the mouth, and is finally distributed to the mucous membrane and papillæ of the tip, edges, and surface of the anterior two-thirds of the tongue. Finally, the motor branches are those (x, x, x) going to the temporal, masseter, and two pterygoid muscles, and that which is distributed (y) to the mylohyoid muscle and the anterior belly of the digastric.

Physiological Properties of the Fifth Pair.—The most prominent and important character belonging to this nerve is that of its *general sensibility*. The regions of the face to which it is distributed, namely, the skin of the cheeks, the eyelids, the tip of the nose, the lips, mucous surfaces of the anterior nares, and especially the tip of the tongue, possess a tactile sensibility of much higher grade than most other regions of the body. The nerve itself, with all its principal branches, is also acutely sensitive to mechanical irritation, and will give rise to indications of sensibility on being wounded or galvanized, under conditions when the spinal nerves generally are nearly or quite inactive.

But the most direct and conclusive experiment bearing on the physiological functions of this nerve and its branches is that of dividing them, either separately or together, by a transverse section. Either the infraorbital or mental nerve may be divided, in the quadrupeds, at the points where they emerge from the corresponding foramina in the maxillary bones. A more decisive method is that of dividing the fifth nerve in the interior of the cranium by a section passing through its trunk at the situation of the Gasserian ganglion. This operation was first performed by Magendie, and has since been frequently repeated by various experimenters. It may be done, upon the cat or the rabbit, by means of a steel instrument with a slender shank and a narrow cutting blade projecting at nearly a right angle from its extremity. The instrument is introduced in a horizontal direction through the squamous portion

of the temporal bone, and pushed inward and a little forward, with its cutting blade laid flatwise upon the surface of the petrous portion, until it strikes the posterior clinoid process. It is then withdrawn slightly, its cutting edge turned downward, and the fifth nerve divided where it crosses the apex of the pyramid formed by the petrous portion of the temporal bone. The instrument is again turned with its cutting blade flatwise, and withdrawn from the skull in this position. When this manœuvre is successfully carried out, all the fibres of the fifth nerve are divided at a single stroke, and the only part of the brain necessarily wounded is the inferior portion of the temporal lobe. The hemorrhage is small in amount, producing only a slight degree of cerebral compression, from which the animal soon recovers.

The immediate effect of this operation is a complete loss of sensibility, upon the operated side, in the integument and mucous membranes about the face. The cornea or conjunctiva can be touched or pricked without exciting any movement of the eyelids; while upon the opposite side these parts retain their natural acuteness of sensibility. A probe may be deeply introduced into the nasal passages, or the upper or lower lip may be pierced throughout its substance with a steel needle, without producing any indication of pain, or eliciting any sign of sensation on the part of the animal. At the same time the power of motion in these parts is unaffected. The eyelids may be opened or closed under the influence of visual impressions, and the movements of the lips and other parts continue to be performed in a nearly natural manner. In the cat, the loss of sensibility and the persistence of the power of motion is readily seen by irritating at different points the integument of the external ear, which in this animal has naturally an acute tactile sensibility. If the point of a steel instrument be brought in contact, upon the operated side, with the anterior part of the ear, which is supplied by fibres from the third division of the fifth nerve, no effect is produced. But if the same irritation be applied to the back part of the ear, which is supplied by the great auricular nerve from the cervical plexus, a vigorous twitching movement is at once excited. According to Longet, the most violent injuries, such as exsection of the eyeball, evulsion of the hairs about the lips, extraction of the teeth, or destruction of the integument by the acutual cautery, may be performed after complete division of the fifth nerve without causing any painful sensation. There is entire anæsthesia of all the parts supplied by filaments of this nerve.

The fifth pair is accordingly the exclusive source of sensibility in the superficial regions of the face, and all parts of the nasal and buccal cavities to which it is distributed.

Painful Affections of the Fifth Pair.—This nerve is also the seat of all the neuralgic painful affections about the head and face. The most common of these is *headache;* which may be general, extending over both sides of the forehead and vertex, or confined strictly to one side. It often seems to be located in the nerves supplying the periosteum,

especially that lining the orbit of the eye, or the frontal sinuses. Where the pain is deep seated, its location may even be in the dura mater or the bones of the skull; since each division of the fifth pair, either before or immediately after leaving the cavity of the cranium, sends backward a slender recurrent branch, destined for the dura mater and the cranial bones. That from the ophthalmic division is traced backward into the tentorium, in the substance of which it ramifies as far as the sinuses bordering its attached edge.

In cases of *toothache*, which depends upon irritation of the dental filaments of the fifth pair, the cause of the neuralgia is usually the decay of the bony substance of the tooth, and consequent exposure of the tooth pulp to external injury or inflammation. It is usually confined to the single tooth affected by decay; but in severe cases the pain may radiate to other teeth in the immediate neighborhood, or may even spread over the entire corresponding side of the maxilla. Neuralgia of the teeth may also be wholly sympathetic in its origin, as where it is caused, like headache, by indigestion, exposure, or fatigue; the pain existing simultaneously in several teeth, without any morbid alteration of their structure.

The most severe and persistent form of neuralgia in this nerve is that known as *tic douloureux;* in which the pain is habitually located in one of its three principal divisions as they emerge upon the face. Here also the pain is not constant, but intermittent, recurring in great severity at longer or shorter intervals, and usually lasting but a few minutes at a time. It is more frequently seated in the upper or middle region of the face, corresponding with the distribution of the supra or infra-orbital nerves.

Lingual Branch of the Fifth Pair.—This branch, which is designated by the special name of the "lingual nerve," possesses an especial interest because it communicates to the mucous membrane of the tongue both the property of tactile sensibility and the special sense of taste. The general sensibility of the tongue is highly developed over the whole of its anterior two-thirds, where it is supplied by the lingual nerve; and at its tip is more acute than in any other region of the body. This sensibility disappears completely on the operated side, together with that of the external portions of the face, when the fifth nerve has been divided in animals in the interior of the cranium; and Longet has found that after section of both lingual nerves, the surface of the anterior two-thirds of the tongue may be cauterized with potassium hydrate or the red-hot iron, without producing any indication of pain. The tactile sensibility of the tongue is of great importance in man, and also in some of the lower animals, as an aid in the process of mastication, by enabling this organ to appreciate the simple physical qualities of the food introduced into the mouth, to perceive when it is uniformly reduced to the proper consistency for swallowing, and to detect any remnants left among folds or crevices of the mucous membrane. These

functions are therefore seriously interfered with by injury or destruction of the sensitive filaments supplying the tongue.

The lingual nerve is also endowed with the special sensibility of *taste.* This function is a difficult one to investigate upon the lower animals, owing to the uncertainty of its external indications and the difficulty of isolating, for the purposes of observation, separate regions of the cavity of the mouth. Experiments upon man, however, which are made with comparative facility, have been performed by Guyot, Vernière, Dugès, and Longet in such a manner as to leave no doubt that the sense of taste is highly developed in those portions of the tongue which are supplied exclusively by the lingual nerve. These experiments consist mainly in applying to different parts of the mucous membrane, in the cavity of the mouth, a small globule of lint, moistened with a solution of some substance, like quinine or colocynth, possessing a distinct taste without irritating qualities. In this way it is ascertained that the point, edges, and superior surface of the tongue, throughout its anterior two-thirds, is capable of perceiving the sensations of taste, without aid from other parts of the buccal mucous membrane. According to the experiments of Bernard and Longet on animals, division of the lingual nerve destroys the faculty of taste as well as that of general sensibility in the corresponding parts of the tongue; and similar observations are quoted by Henle, after section of this nerve in the human subject.

Muscular Branches of the Fifth Pair.—These branches, as enumerated above, are given off from the inferior maxillary division, for the most part a short distance below its exit from the skull, and are distributed to the temporal, the masseter, and the external and internal pterygoid muscles; while the mylohyoid branch, which separates from the trunk somewhat farther down, supplies the muscle of the same name as well as the anterior belly of the digastric. All these nerves are, therefore, concerned in the movements of mastication. The most powerful of the muscles to which they are distributed, namely, the temporal and the masseter, act by bringing the teeth of the lower jaw forcibly in contact with those of the upper. The contraction of the two pterygoid muscles produces a lateral grinding movement, by which the trituration of the food is accomplished; and finally those supplied by the mylohyoid branch facilitate the partial separation of the jaws, to allow a repetition of the former motions. In different species of animals these movements vary in their relative importance. In the carnivora, it is the closure of the jaws which preponderates over the rest, enabling the animal to seize and tear his prey, by means of the pointed canine and sharped-edged molar teeth. In the herbivora, on the other hand, the lateral grinding movements are more important for the complete comminution of the seeds, grains, or other hard vegetable tissues upon which they feed. In man, both movements coexist in a nearly equal degree.

The movements of mastication are accordingly paralyzed by section

of the fifth pair, and are the only muscular functions directly interfered with by this operation. There is a difference, however, in the ultimate consequences which follow paralysis of mastication, according to the species of animal affected. If the fifth pair, or its inferior maxillary division, were destroyed on both sides in either a carnivorous or herbivorous animal, death would follow from inanition, owing to the impossibility of preparing the food for deglutition. If the injury were inflicted upon one side only, it would be equally fatal in the herbivora, by preventing the alternate lateral movements of the jaw; while in a carnivorous animal the vertical movements, which are more important, would be less seriously affected, since they might still be performed, though imperfectly, by the muscles of the opposite side.

But the most peculiar secondary result of paralysis of the muscles of mastication on one side is seen in the rodentia. In these animals the most important teeth are the four incisors, two in the upper and two in the lower jaw, which are used for gnawing through hard substances, and which grow continuously from the tooth-pulp below, thus supplying the waste caused by wearing away their edges. The teeth move against each other in an exact vertical plane, the upper and lower incisors on each side meeting each other, and thus by mutual attrition keeping their chisel-like edges at a corresponding level. If the fifth nerve be divided in these animals, the lower jaw becomes deviated toward the operated side in consequence of the paralysis of the corresponding petrygoid muscles. The edges of the four incisor teeth then no longer correspond with each other, but are so shifted that one of those in the upper and one in the lower jaw do not meet with any opposing edge, and are consequently no longer worn away. According to the experiments of Bernard on rabbits, the line of junction between the edges of the teeth, instead of being horizontal, then becomes oblique, being directed from above downward, from the operated toward the sound side, and the same fact has been observed by Flint.[1] If the animal survive for a considerable time, the teeth which are no longer worn away, as they continue to grow from the tooth-pulp below, may become excessively elongated. We have seen an instance in the woodchuck (Arctomys monax) of lateral deviation of the teeth from a reunited fracture of the lower jaw, in which the upper incisor on one side and the lower on the other had increased to five or six times their natural length, and had probably caused the death of the animal by penetrating the soft parts about the head and interfering with the movement of the jaws.

Anastomotic Branches of the Fifth Pair.—Although the separate regions of the face are supplied in a general way by the three great divisions of this nerve, there is yet more or less communication between them by intermingled filaments from different sources, and the separate branches of each division communicate with considerable frequency. Thus the infra-orbital nerve, which sends filaments to the lower eyelid,

[1] Physiology of Man; Nervous System. New York, 1872, p. 198.

inosculates by a distinct twig with one of the nasal branches of the ophthalmic division. The integument of the nose is supplied by the nasal branches of the ophthalmic division, and also by those coming from the infraorbital nerve. The upper and lower lips are supplied both from the infraorbital and mental nerves on the outside, and from the terminal filaments of the buccinator nerve on the inside; and the temporal region receives branches both from the superior and inferior maxillary divisions. A most important anastomotic branch of the fifth pair is that which its inferior maxillary division sends to the facial nerve (Fig. 174, *f*), and by means of which it supplies sensitive filaments to the great motor nerve of the face. As a general rule, nerves which are distributed exclusively to muscles receive at some part of their origin or course sensitive filaments which accompany them to their destination. The muscular tissue consequently has a certain degree of sensibility; and it is this sensibility, sometimes called the "muscular sense," which enables us to appreciate the existence and degree of contraction in any particular muscle or group of muscles. Many of the sensitive filaments supplied to the facial nerve by the communicating branch of the fifth are undoubtedly destined to reach the muscles of the face with the terminal branches of this nerve; but there are also abundant anastomoses between the facial nerve and the fifth near the final distributions of the latter nerve. These anastomoses are quite numerous, between the branches of the infraorbital and mental nerves and those of the facial; and certain regions of the integument may, therefore, be supplied with sensibility by filaments from both these sources. The observations of L'Etiévant[1] have shown that it is impossible to abolish the sensibility of any extended region of the face by section of either division of the fifth pair alone. A complete anæsthesia can only be produced by division of the whole nerve within the cranial cavity. This destroys at once not only the sensibility supplied directly by the fifth pair, but also that communicated to the facial by its anastomotic branch.

According to Henle, there is still a portion of the side of the face which may derive a certain degree of sensibility, apart from that due to the fifth pair, from the great auricular nerve of the cervical plexus; since the anterior branch of this nerve, after supplying the under part of the lobe of the ear, sends some slender filaments anteriorly to the integument of the cheeks, running in some instances as far forward as the neighborhood of the malar bone.

Influence of the Fifth Pair on the Special Senses.—The results of experiment show that this nerve has an important influence upon the special senses, since they are always more or less interfered with, and in some instances practically destroyed, by its division or injury. This influence, however, is mainly not a direct but an indirect one; and shows itself by a disturbance of nutrition in the tissues of the organ. For the perfect action of any of the special senses, two different conditions are

[1] Traité des Sections Nerveuses. Paris, 1873, p. 179.

requisite: first the peculiar sensibility of its own special nerve, and secondly the integrity of the component parts of the organ itself. As the nutrition of the organ is affected by injury or disease of the fifth pair, this necessarily causes a derangement in its physiological action and thus interferes with the exercise of the special sense belonging to it. These effects seem to depend, not so much upon the division of the ordinary sensitive fibres of the fifth nerve, as of those which are derived from the nerve cells of the Gasserian ganglion, or which are supplied by the fifth pair to the special sympathetic ganglia connected with the organs of sense.

Influence on the Sense of Smell.—The nasal passages are supplied by two different nerves derived from the cerebro-spinal system, namely, the olfactory nerve distributed to their upper portions, and endowed with its own special sensibility; and the nasal branches of the fifth pair, distributed in the lower portions, to which they communicate the general sensibility of the mucous membrane. The mucous membrane also contains filaments from the spheno-palatine ganglion of the sympathetic; and this ganglion receives its sensitive root from the superior maxillary division of the fifth pair.

The general sensibility of the nasal passages may accordingly remain after the special sense of smell has been destroyed. If the fifth pair, however, be divided, not only is general sensibility destroyed in the Schneiderian membrane, but a disturbance also takes place in its nutrition, by which the power of smell is also lost. The mucous membrane becomes swollen, and the nasal passage is obstructed by an accumulation of mucus. According to Longet, the membrane also assumes a fungous consistency, and is liable to bleed at the slightest touch. The effect of this alteration is to blunt or destroy the sense of smell. It is owing to a similar condition of the mucous membrane that the power of smell is impaired in cases of influenza. The olfactory nerves become inactive in consequence of the alteration in their mucous membrane and its secretions.

Influence on the Sense of Sight.—The anterior parts of the eyeball are also supplied with nerves of ordinary sensibility from the fifth pair, while the special impressions of light are transmitted exclusively by the optic nerve. In addition, the iris and cornea are supplied by filaments coming from the ophthalmic ganglion of the sympathetic, which receives its sensitive root from the fifth pair. If this nerve be divided within the cranium, by a section passing in front of or through the Gasserian ganglion, a change of nutrition often follows in the cornea, by which its tissue becomes the seat of vascular congestion and ulceration, and which frequently goes on to complete and permanent destruction of the eye. These changes may be observed in the cat, after intracranial section of the fifth nerve by the usual method. Immediately after the operation the pupil is contracted and the conjunctiva loses its sensibility. At the end of twenty-four hours the cornea begins to become opaline, and by the second day the conjunctiva is visibly congested,

and discharges a purulent secretion. This process, after commencing in the cornea, increases in intensity and spreads to the iris, which becomes covered with an inflammatory exudation. The cornea grows more opaque, until it is at last altogether impermeable to light, and vision is consequently suspended. Sometimes the diseased action goes on until it results in sloughing and perforation of the cornea and discharge of the humors of the eye; sometimes, after a few days, the inflammatory appearances subside, and the eye is finally restored to its natural condition.

According to the observations of Bernard, although these consequences usually follow division of the fifth nerve when performed at the situation of the Gasserian ganglion, or between it and the eyeball, they are either retarded in their appearance or altogether wanting when the section is made posteriorly to the ganglion, between it and the base of the brain. This indicates that the influence exerted by this nerve upon the nutrition of the eyeball does not reside in its own proper fibres, but in additional filaments derived from the Gasserian ganglion.

Influence on the Sense of Taste.—The lingual branch of the fifth pair communicates to the anterior portion of the tongue at the same time its acute general sensibility and its sensibility of taste; both of which are, of course, abolished by its division. Whether both kinds of sensibility reside in the same or in different fibres cannot yet be determined; but cases which have been observed in man, of impairment of the sense of taste, while tactile sensibility remains entire, make it possible that there may be two distinct sets of fibres in the lingual nerve, one devoted to general sensibility, the other to that of taste. However that may be, it is evident that the exercise of the sense of taste is facilitated by the presence of general sensibility in the mucous membrane of the tongue, and is influenced by the state of the local circulation and the buccal secretions. In a tongue which is dry or coated, as in the febrile condition, taste is practically abolished; as much so as the sense of sight from opacity of the cornea. The sense of taste, accordingly, depends for its exercise, not only upon the special sensibility of the lingual nerve, but also upon all the physiological conditions requisite for the integrity of the mucous membrane.

Influence upon the Sense of Hearing.—The influence of the fifth pair upon the sense of hearing is less certainly known than that exerted upon the other special senses, and is only to be surmised from the similarity of its anatomical relations. This nerve provides for the general sensibility of the external ear by twigs from its auriculo-temporal branch, which supply the skin of the anterior border of the concha and that of the anterior wall of the external auditory meatus. Its relation with the deeper parts of the organ is established by means of the otic ganglion of the sympathetic, which receives a few short fibres from the inferior maxillary division of the fifth pair, and which sends a filament backward to join the tympanic plexus on the inner surface of the membrane of the tympanum. This plexus is also supplied with filaments from

the ganglion situated upon the trunk of the glosso-pharyngeal nerve; and is consequently made up of interlacing fibres derived from both these sources. Its peripheral sensitive fibres terminate in the mucous membrane lining the cavity of the middle ear. The secretions, both of this cavity and of the external auditory meatus, are important for the preservation of the integrity of the parts and for the mechanism of audition; and they are undoubtedly in great measure under the control of the nervous supply, of which a considerable portion is derived from the fifth pair.

Sixth Pair. The Abducens.

The abducens nerve, so called because it is distributed only to the single muscle which causes the movement of abduction of the eyeball, originates mainly from a collection of gray matter on the floor of the fourth ventricle, near its widest part and at a point corresponding with the posterior section of the pons Varolii. It is situated next the median

Fig. 175.

TRANSVERSE SECTION OF THE FLOOR OF THE FOURTH VENTRICLE of the Human Brain, showing the nucleus and roots of the abducens and facial nerves.—Nf, Nucleus of gray matter. VI′, Fibres of the abducens nerve (6th pair). VII′, Fibres of the facial nerve (7th pair). VII″, Bundle of longitudinal fibres, connected with the root of the facial nerve. R, Raphe, at the median line, showing transverse or decussating fibres from the facial nerve roots. Magnified 35 diameters. (Henle.)

line, and is indicated on each side by a longitudinal prominence, known as the "fasciculus teres." This collection of gray matter is the *common nucleus of the abducens and facial nerves;* since the fibres of both these nerves are traced to a connection with it, although running in somewhat different directions. The fibres of the abducens, as shown by Dean, Meynert, and Henle, originate from the inner border of the nucleus without showing any apparent decussation with those of the opposite side. They then pass almost directly downward and forward, in a vertical longitudinal plane, through the substance of the tuber annulare, to their point of emergence at the base of the brain, at the posterior edge

of the pons Varolii. From this point, the nerve, which is about two millimetres in thickness, runs nearly straight forward, beneath the under surface of the pons, passes, in company with the oculomotorius and patheticus, along the wall of the cavernous sinus and through the sphenoidal fissure, into the cavity of the orbit, where it terminates in the external straight muscle of the eyeball.

Physiological Properties of the Abducens.—The physiological properties of this nerve have been examined, in the experiments of Longet on rabbits, and in those of Chauveau on rabbits and horses, by irritating its trunk within the cranium and at its point of emergence from the pons Varolii. The abducens is thus shown to be, at its origin and for some distance beyond, exclusively a motor nerve; since its galvanization produces at once continued contraction in the external straight muscle of the eyeball, and mechanical or other irritation applied to its fibres causes no indication of suffering. In the experiments of Longet, which were performed upon the living animal, the difference in this respect between the abducens nerve and the trigeminus was very marked; irritation of the trigeminus always giving rise to signs of acute sensibility, while that of the abducens had no other effect than local muscular contraction.

Division of this nerve causes internal strabismus from paralysis of the external straight muscle, and loss of the lateral motion of the eyeball in a horizontal plane; although its vertical movements are still preserved, owing to the continued activity of the oculomotorius nerve. Cases of internal strabismus, in man, are recorded, with the accompanying symptoms mentioned above, which were apparently due to compression of the abducens nerve by morbid growths within the cranial cavity.

Seventh Pair. The Facial.

With regard to the innervation of the external parts of the face, this nerve holds an equal rank with the fifth pair, and may be regarded as complementary to it in physiological endowments. As the fifth pair is the nerve of sensation for the integument of this region, the facial is the motor nerve for its superficial muscles. It is the nerve of facial expression, by which the features are animated in their varying movements, corresponding with the different phases of mental or emotional activity. Although at its origin an exclusively motor nerve, it receives, soon after its emergence from the cranium, a communicating branch from the fifth pair, which gives to it, and to the muscles in which it terminates, a certain share of sensibility.

The facial nerve has its principal source in a collection of gray matter, which has already been described as also giving origin to the fibres of the abducens (Fig. 175). This nucleus extends for a short distance longitudinally along the floor of the fourth ventricle near the median line, as a layer about 1.5 millimetre in thickness, and containing, according

to Dean,[1] stellate, oval, or fusiform nerve cells, among which the nerve fibres penetrate. The nucleus constitutes, at this situation, the gray matter of the "fasciculus teres." The fibres of the abducens and facial nerves are given off from its internal and external borders respectively; those of the abducens passing directly downward through the tuber annulare, near the median plane, those of the facial first passing outward and then bending downward, to reach their point of emergence at the posterior edge of the lateral portion of the pons Varolii.

According to Dean, Meynert, and Henle, a considerable portion of the root fibres of the facial nerve communicate, either directly or through the nucleus, across the median line, with the opposite side of the brain.

After emerging from the posterior edge of the pons Varolii, the facial nerve, in company with the auditory, passes into and through the internal auditory meatus. It then enters, by itself, the aqueduct of Fallopius, and, following the course of this canal through the petrous portion of the temporal bone, comes out at the stylomastoid foramen and turns forward upon the side of the face. It spreads out between the lobules of the parotid gland into a number of branches, which by their mutual interlacement form the well-known "parotid plexus," or "pes anserinus," of this nerve. Its branches then diverge upward, forward, and downward, to be distributed to the superficial muscles of the facial region. It also supplies, by branches given off immediately after its emergence from the stylomastoid foramen, the muscles of the external ear, as well as the stylohyoid and the posterior belly of the digastric; and by a twig which descends below the jaw to the submaxillary region, it supplies filaments to the upper part of the platysma myoides muscle, and communicates with an ascending branch of the superficial cervical nerve from the cervical plexus.

Physiological Properties of the Facial Nerve.—The facial is shown, by the result of abundant corresponding investigations, to be, at its origin and in its main physiological characters, an exclusively motor nerve. Not only is the tactile sensibility of the facial region immediately destroyed by the section of the fifth pair within the skull, though the facial itself remain uninjured, but, according to the experiments of Magendie and Bernard, the trunk of this nerve, when irritated at its source in the living animal, after opening the cranial cavity, shows no sign of sensibility, although that of the sensitive cranial nerves is at the same time perfectly manifest. On the other hand, Chaveau has found that in the recently killed animal, galvanization of the intracranial portion of the facial nerve causes at once contraction of the muscles of the face and of the external ear. This nerve is accordingly, at its source, insensible and excitable.

Furthermore, the most decisive results are obtained from division of the facial nerve at various parts of its course. This may be done, in

[1] Gray Substance of the Medulla Oblongata and Trapezium. Washington, 1864, pp. 58, 61.

most quadrupeds, at the point of exit of the nerve from the stylomastoid foramen, or, as practised by Bernard, during its passage through the aqueduct of Fallopius, by means of a cutting instrument introduced into the cavity of the tympanum, thus reaching the nerve through

Fig. 176.

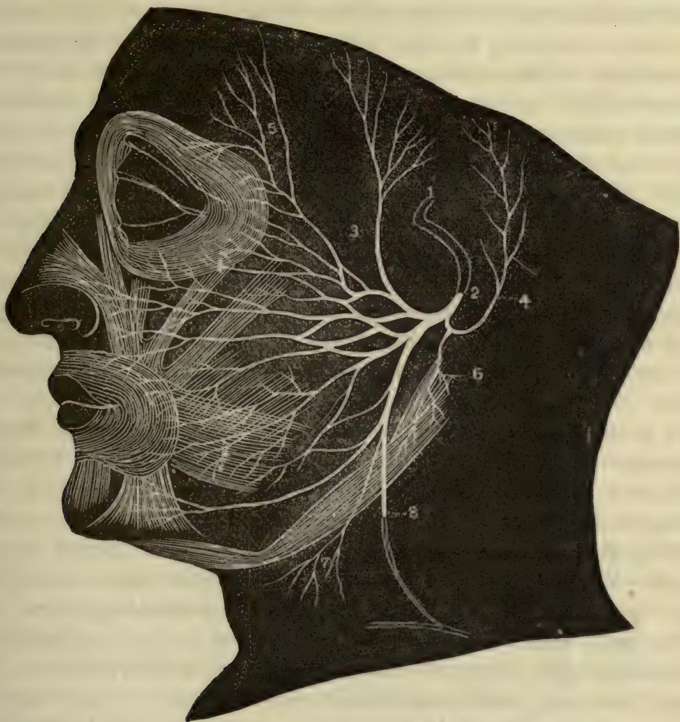


DIAGRAM OF THE FACIAL NERVE AND ITS DISTRIBUTION.—1. Facial nerve at its entrance into the internal auditory meatus. 2. Its exit, at the stylomastoid foramen. 3, 4. Temporal and posterior auricular branches, distributed to the muscles of the external ear and to the occipitalis. 5. Branches to the frontalis muscle. 6. Branches to the stylohyoid and digastric muscles. 7. Branches to the upper part of the platysma myoides. 8. Branch of communication with the superficial cervical nerve of the cervical plexus.

its upper wall. The effect of this section is to paralyze at once all the superficial muscles of the face on the corresponding side. The visible effects vary in the different facial regions, according to the function of the muscles which have lost their power of motion.

Effect upon the Eye.—The orbicularis oculi being paralyzed, the eye upon the affected side cannot be closed, but remains permanently open; even, according to the observation of Bernard, while the animal is asleep. This depends upon the fact that the two muscles serving to open and close the eyelids are animated by two different nerves; the levator palpebræ superioris, which lifts the upper eyelid, being supplied by the oculomotorius, while the orbicularis oculi receives its nervous

filaments from the facial. After paralysis of this nerve, therefore, complete closure of the lids becomes impossible, although the movements of the eyeball are unaffected, and the pupil is capable of dilatation and contraction as before.

At the same time the motion of winking is suspended upon the affected side. This movement is an involuntary reflex action, excited by the contact of air with the surface of the cornea, and the accumulation of the tears along the edge of the lower eyelid. At short intervals this produces an instantaneous contraction of the orbicularis, by which the edges of the eyelids are brought together, and again immediately separated; thus spreading the moisture of the lachrymal secretion uniformly over the cornea and protecting its surface from dryness or irritation. After section of the facial nerve, this movement ceases, and on thrusting a solid body suddenly toward the face of the animal it can be seen that the eye on the sound side instinctively closes, while the other remains open. Even touching the conjunctiva or the cornea on the operated side fails to cause contraction of the eyelids, although the animal shrinks and the eyeball turns in the orbit; showing that the motor power of the orbicularis alone has been affected while sensibility remains.

Two precisely opposite effects, accordingly, are produced upon the movements of the eye, by section of the fifth nerve, or its ophthalmic branch, and by that of the facial. After division of the fifth nerve, touching the cornea fails to produce closure of the eyelids because the sensibility of its surface has been destroyed, though the power of motion remains. When the facial has been divided, it is the muscular action which is paralyzed, the sensibility of the parts remaining entire.

Effect on the Nostrils.—In some animals, as in man, the nostrils are more or less rigid and nearly inactive in the ordinary condition. They expand, however, with considerable vigor when the movements of respiration are increased in frequency, or when the air is forcibly inspired to assist in the sense of smell. In many species, furthermore, as in most graminivorous quadrupeds, and especially in the horse, they alternately expand and collapse in a regular and uniform manner, with each inspiration and expiration; executing in this way a series of respiratory movements synchronous with those of the chest and abdomen. Even in man the expansion of the nostrils, at the time of inspiration, becomes very marked whenever the breathing is hurried or laborious, owing to increased muscular exertion or to any accidental obstruction of the air-passages.

All these movements are suspended by section of the facial nerve. The muscles by which they are performed being paralyzed, the nostril on the affected side becomes flaccid, and, instead of opening for the admission of air into the nares, it collapses and forms more or less of an obstruction to its entrance. As the partial dyspnœa thus induced tends to accelerate the breathing, the paralyzed nostril is still further compressed by the air in the movement of inspiration; while at the

time of expiration, on the other hand, it is forced outward by the exit of the air. The natural movements of the nostril in respiration, are therefore reversed by paralysis of the facial nerve. In the normal condition they exhibit an active expansion in inspiration, and a partial collapse in expiration. After section of the nerve the nostril collapses in inspiration, and partially opens in expiration; moving passively inward and outward, like an inert valve, with the changing direction of the current of the air.

Effect on the Lips.—In the lower animals generally, but especially in the herbivora, the movements of the lips are mainly serviceable in the prehension of the food; and if these movements be paralyzed on the two sides at once, by section of both the facial nerves, the consequent incapacity to introduce food into the mouth may be sufficiently serious to cause death by inanition. In the carnivora the motions of retraction and elevation of the lips, by which the canine teeth are uncovered, have also a marked effect on the expression of the face. In most of these animals, after division of the facial nerve, the change in the appearance of the corresponding side, even in the quiescent condition, is distinctly perceptible. The lips are flaccid and motionless, and the corner of the mouth hangs down and cannot be completely closed, owing to the paralysis of the orbicularis oris muscle.

Effect on the Ears.—In most of the quadrupeds the action of the external ears is much more important than in man, owing to their superior mobility and the greater development of the corresponding muscles. In all, the varying position of these organs is of great influence in modifying the expression; and their rapid and extensive movements are also serviceable as an essential aid to the sense of hearing. When the facial nerve has been divided, the ear on the corresponding side becomes flaccid and motionless; and in species where the organ is long and narrow, as in the hare and rabbit, it can no longer be maintained in the erect position.

All the superficial muscles accordingly of the head and face, which are supplied by filaments from this nerve, are paralyzed by its section; while the sensibility of the skin, in the corresponding parts, is preserved entire.

Facial Paralysis in Man.—Facial paralysis, from disease involving the nerve itself, its sources of origin in the brain, or the walls of its bony canal in the cranium, is not an uncommon affection in the human subject. It is usually confined to one side, being limited by the median line, and produces accordingly a marked difference in the appearance of the two sides of the face. In particular cases, where the cause of the difficulty is located in the branches of the nerve, certain portions of the muscular apparatus may be affected to the exclusion of others; and the muscles about the lips may be paralyzed without any perceptible loss of motion in the parts above. Or the affection may be fully developed in one region of the face, and only partial in the remainder. But when the disease is seated upon the trunk of the nerve within the

aqueduct of Fallopius, or involves the whole of its central origin, its consequences extend uniformly over one side of the face, forming a complete unilateral facial paralysis.

The external signs of paralysis of the facial nerve from disease in man are, in general, the same with those which follow experimental division of this nerve in animals. The main peculiarity depends upon the greater development of the facial muscles in man as the organs of expression. The most marked effect, therefore, of this disease in the human subject, is a loss of expression on the paralyzed side of the face.

Fig. 177.

Facial Paralysis of the right side.

All the features have a collapsed and flaccid appearance. The eyelids remain motionless, and the eye is constantly open, not only on account of the impossibility of bringing down the upper eyelid, but also because the lower lid sinks down more or less below the level of the cornea; thus giving to the eye a staring, vacant appearance. The act of winking is no longer performed upon the affected side. Owing to the paralyzed condition of the frontalis and superciliary muscles, all the characteristic lines and wrinkles on this side disappear, and the forehead and eyebrow become smooth and expressionless. The same thing is true of the

cheek, which, as well as the nostril, is flattened and collapsed. The corner of the mouth hangs downward, and the lips cannot be kept in contact with each other at this point, sometimes allowing the saliva to escape by drops from the cavity of the mouth.

Beside these symptoms there is also, in man, a *deviation of the mouth towards the sound side*, owing to the facial muscles on that side being no longer antagonized by those opposite. In many instances this deviation is not observable during a state of quiescence, since both sets of muscles are then equally relaxed; and it becomes evident only when the patient begins to move the muscles of the sound side, as in speaking or laughing, or when the emotions are excited. But in some cases, where the face has naturally an abundance of expression, the distortion of the features, and the consequent difference between the two sides of the face, are distinctly shown even in the quiescent condition, and become still more marked when the patient is excited or engages in conversation.

Another secondary effect of facial paralysis in man is *difficulty in drinking and in mastication.* The first is due to the impossibility of contracting the orbicularis oris on the affected side; so that the lips at this corner of the mouth cannot be kept firmly in contact with the sides of the goblet. The consequence is that a portion of the fluid escapes and runs over the lower part of the face, unless the patient take the precaution to aid the paralyzed part by pressure with his fingers. The difficulty in mastication is not owing to any paralysis of the muscles moving the lower jaw. These muscles are animated by the inferior maxillary division of the fifth pair, and are unaffected in disease of the facial nerve. It results from the paralysis of the buccinator muscle, and the relaxed condition of the side of the cheek. In consequence of this, the food in mastication lodges partially in the space between the outside of the gum and the inside of the cheek; and the patient is often obliged to remove it by mechanical means in order to complete its mastication.

The loss of power in the orbicularis oris also produces an *imperfect articulation.* The lips cannot be brought together with sufficient precision, and consequently the labials, such as B and P, are imperfectly pronounced. If the paralysis be bilateral, existing on both sides of the face at a time, cases of which have been sometimes observed, the features are no longer deviated from their symmetrical position, but the difficulty of articulation becomes much increased, extending not only to the labials proper, but also to such of the vowels, as O and U, which require a certain contraction of the orbicularis oris. This affection is distinguished from that known as "glosso-labio-laryngeal paralysis," in which articulation is also impaired. In the latter disease, which is of central origin, the paralysis affects the muscles of the tongue and larynx as well as those of the lips; in facial paralysis it is confined to those which receive their filaments from the facial nerve. Facial paralysis may therefore exist without danger to life.

Crossed Action of the Facial Nerve.—The results of minute examination of the mode of origin of this nerve give indications of a transverse communication by decussating nerve fibres, between its nucleus at the floor of the fourth ventricle and the opposite side of the tuber annulare. It has not yet been possible, however, to follow with certainty the individual fibres to their termination, or to decide whether the decussating fibres are part of the original root fibres which have simply passed through the nucleus, or whether they originate anew from the nerve cells of the nucleus and thence pass to the opposite side. The opinion usually adopted by anatomists from the examination of microscopic sections is that a part of the fibres of each cranial nerve root terminate in the nucleus of the same side, and a part cross over, as decussating fibres, to the opposite side. This is plainly shown in the case of the patheticus, which is the only one of the cranial nerves, beside the optic, exhibiting a distinct decussation of its root fibres outside their connection with the nucleus.

That the action of the facial nerve is in great part a crossed action is evident from the results of pathological observation. Facial paralysis is a frequent accompaniment of hemiplegia; and in the great majority of instances, that is, when the cerebral lesion is situated above the tuber annulare, the hemiplegia of the body and limbs and the paralysis of the face are upon the same side with each other. The injury to the brain, therefore, in these cases, produces both hemiplegia and facial paralysis on the opposite side. When the injury is seated lower down, on the contrary, in the substance of the tuber annulare, it may affect at the same time the roots of the facial nerve outside its nucleus, and the longitudinal tracts of the anterior pyramids above their decussation; and may cause in this way a facial paralysis on the same side and hemiplegia on the opposite side. It thus appears that the facial paralysis is on the same side with the injury when this is seated externally to the nucleus, and on the opposite side when it is seated above the nucleus and near the central parts of the brain. This shows that for a large part of its functions, the action of the facial nerve is entirely a crossed action.

The communication, however, between the nucleus and the opposite side of the brain, upon which this crossed action depends, does not affect all the fibres of the nerve, nor the whole of the physiological functions which are under its control. The only decussation of the nerve fibres connected with the facial known to exist, is that which takes place at the raphe on the floor of the fourth ventricle. If all the fibres of the nerve root or their continuations crossed at this point, from right to left and from left to right, then a longitudinal section at the raphe, following the median line between the two nuclei, would completely paralyze both sides of the face at the same time. But this effect is not produced; since, in the experiments of Vulpian,[1] who has performed this

[1] Leçons sur la Physiologie du Système Nerveux. Paris, 1866, p. 480.

operation on dogs and rabbits, the animals were still capable of winking with both eyes; only the action of the two nerves was no longer simultaneous, and the closure of each eye was performed at irregular intervals independently of the other.

It is evident, therefore, that the reflex act of winking takes place for each eye upon the same side, undoubtedly in the gray matter of the facial nucleus; and the two nuclei habitually act in harmony with each other by means of the commissural fibres passing between them. But the mental and emotional influences, which cause the movement of the features in expression or in voluntary acts, are transmitted by decussating fibres from the opposite side of the brain.

This is still further indicated by the different effects caused by peripheral and central lesions of the facial nerve. In man, as in animals, if this nerve be divided or destroyed during or after its passage through the aqueduct of Fallopius, all the movements of the facial muscles are paralyzed together. But in cases of facial paralysis depending upon a lesion in the cerebrum itself, that is, above the situation of the nucleus, it is generally observed, according to Vulpian and Hammond,[1] that the loss of movement is not complete; but that, while all the other parts of the face are paralyzed, the patient retains the power of winking on the affected side. This peculiarity is even given as a means of diagnosis between facial paralysis dependent upon injury of the nerve itself and that caused by a lesion in the brain.

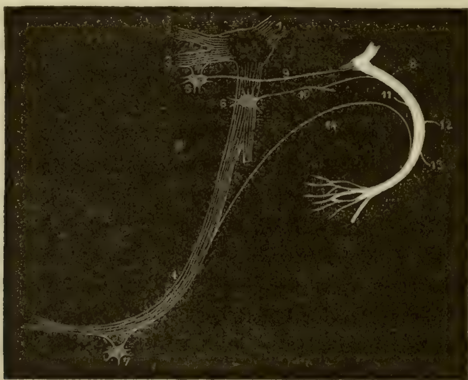
Sensibility of the Facial Nerve.—Although this nerve is exclusively motor at its origin, it receives filaments of communication from the fifth pair, which give it a certain degree of sensibility. The most important of these branches, given off from the inferior maxillary division of the fifth nerve, joins the facial soon after its emergence from the stylomastoid foramen, and runs forward with its principal branches and ramifications. The facial nerve, therefore, according to the united testimony of all modern experimenters, if examined upon the side of the face, is found to be sensitive to mechanical irritations, although the degree of its sensibilty is much less than that of the fifth pair. Owing to this communication, the pain, in cases of tic douloureux, sometimes follows the course of the horizontal branches of the facial nerve. The proof, however, that the sensitive fibres of this nerve are derived from its anastomoses and do not orginally form a part of its trunk, is that the sensibility of the facial regions to which it is distributed disappears completely after division of the fifth pair, notwithstanding that the facial nerve itself remains entire.

Beside the principal communication above mentioned, this nerve contracts abundant anastomoses, at the anterior part of the face, with the radiating filaments of the supraorbital, infraorbital, and mental branches of the fifth pair.

[1] Diseases of the Nervous System. New York, 1871, p. 78.

Twigs and Communications of the Facial Nerve in the Aqueduct of Fallopius.—While passing through its canal in the petrous portion of the temporal bone, the facial nerve gives off a number of slender filaments by which it communicates with other nerves or with ganglia belonging to the sympathetic system. The physiological character of most of these filaments is imperfectly understood; but certain facts have been established in regard to them, and they are of interest because they are usually involved in injury or disease of the nerve within its bony canal, and thus other secondary symptoms are produced in addition to those of external facial paralysis.

Fig. 178.



THE FACIAL NERVE AND ITS CONNECTIONS, within the aqueduct of Fallopius.—1. Fifth nerve, with the Gasserian ganglion. 2. Ophthalmic division of the fifth nerve. 3. Superior maxillary division of the fifth nerve. 4. Lingual nerve. 5. Sphenopalatine ganglion. 6. Otic ganglion. 7. Submaxillary ganglion. 8. Facial nerve in the aqueduct of Fallopius. 9. Great superficial petrosal nerve. 10. Small superficial petrosal nerve. 11 Stapedius branch of facial nerve 12. Branch of communication with pneumogastric nerve. 13. Branch of communication with glossopharyngeal nerve. 14. Chorda tympani.

At the elbow formed by the anterior bend of the facial nerve, soon after its entrance into the aqueduct of Fallopius, there is a minute collection of gray matter, known as the "ganglion geniculatum." From this point a slender filament, the *great superficial petrosal nerve* (Fig. 178, $_9$), runs forward, passing obliquely through the base of the skull, and terminates in the sphenopalatine ganglion. This ganglion, which is also in connection, by another root, with the superior maxillary division of the fifth nerve, lends filaments to the mucous membrane of the posterior part of the nasal passages and that of the hard and soft palate and to the levator palati and uvular muscles; that is, to the dilators of the isthmus of the fauces.

This nerve, which forms communication between the facial and the sphenopalatine ganglion, is without doubt the motor root of the ganglion, supplying motive force from the facial to the muscular branches given off from it beyond. This conclusion is derived from the phenomena of paralysis of the palatal muscles accompanying certain cases

of facial paralysis, where the lesion is deep seated. The paralysis is recognized by an incapacity to lift the soft palate, which hangs down in a passive manner, and by the deviation of the uvula, which, according to the observations recorded by Longet, is always toward the sound side. The levator palati, and especially the uvular muscle, being paralyzed, its fellow in contracting draws the uvula into an oblique position, with its point directed toward the non-paralyzed side. As there is no other communication between the facial nerve and the palatal muscles, than that through the sphenopalatine ganglion by the great superficial petrosal nerve, this nerve must be regarded as containing motor fibres running from the facial to the ganglion.

A little below the origin of the last-mentioned filament, the facial nerve gives off a second, the *small superficial petrosal nerve* ($_{10}$), which communicates both with the otic ganglion and with the plexus of nerve filaments on the inner wall of the tympanum, known as the "tympanic plexus," which supplies nerve fibres to the lining membrane of the tympanic cavity, while the otic ganglion sends a motor filament to the tensor tympani muscle.

From the concave border of the facial nerve, as it bends downward, a fine motor filament, the *stapedius branch* ($_{11}$), passes forward to supply the stapedius muscle. The facial nerve, therefore, in this part of its course, has an influence on the mechanism of hearing, through the muscles which regulate the position of the bones of the middle ear, and consequently the tension of the membrana tympani. This influence is exerted directly by its stapedius branch, and indirectly, through the otic ganglion, by the filament supplied to the tensor tympani. Cases of facial paralysis have been known to be accompanied, sometimes by partial deafness, and sometimes by abnormal sensibility to sonorous impressions; but it has not been determined how far these symptoms were due to the implication of other parts, or how far to paralysis of the muscles of the middle ear from disease of the facial.

From its descending portion, the facial nerve gives off two small branches of communication ($_{12,\ 13}$), one to the *pneumogastric* and one to the *glossopharyngeal* nerve. They are usually regarded as motor filaments, which transmit to these two nerves the power of causing muscular contraction. This seems nearly certain in regard to the branch communicating with the glossopharyngeal nerve; since Cruveilhier describes a separate filament of the facial passing to the styloglossus and palato-glossus muscles, and Longet cites an instance in which a branch of the facial, on one side, without making any connection with the glossopharyngeal nerve, was distributed directly to the palato-glossal and glossopharyngeal muscles; that is, to the constrictors of the isthmus of the fauces.

Finally the facial nerve, shortly before its exit from the stylomastoid foramen, gives off from its concave border another slender branch of considerable interest, the *chorda tympani* ($_{14}$). It first passes upward and forward, in a recurrent direction, traverses the cavity of the tym-

panum near the inner surface of the membrana tympani, curves downward and forward, and joins the descending portion of the lingual nerve. It is certain that some of its fibres again leave the lingual nerve at the situation of the submaxillary ganglion, to reach this ganglion and the tissue of the submaxillary gland; and it is also certain that some of them continue onward with the lingual nerve, and accompany it to its distribution in the tongue.

The most positive knowledge in our possession with regard to the physiological character of the chorda tympani is that it is distinctly a *motor nerve*, *influencing the acts of circulation and secretion.* This results from the numerous experiments of Bernard[1] on the dog and cat, which show that, in these animals, galvanization of the chorda tympani increases at the same time the activity of the circulation and the secretion of saliva in the submaxillary gland. The gland, with its excretory duct and nervous connections, is exposed in the living animal. It is then seen that the introduction of vinegar into the fauces causes, by reflex action, an increased current of blood through the vessels of the gland, and excites an abundant flow of submaxillary saliva. But if the chorda tympani be tied or cut across, the action above described no longer takes place, and the gland remains inexcitable under the influence of a sapid substance introduced into the fauces. On the other hand, if the peripheral extremity of the nerve be galvanized, this stimulus excites the circulation and secretion as before; and the same effect is produced by stimulating, either the lingual nerve itself, or the filament which it sends to the submaxillary gland. Finally, while section of the chorda tympani in the cavity of the tympanum, or evulsion of the facial nerve from the aqueduct of Fallopius, will arrest the secretive activity of the submaxillary gland, section of the facial at the stylomastoid foramen does not have this effect, but only paralyzes the muscles of the face. A difference accordingly exists, in the effects produced by injury of the facial nerve, according to its location, within the aqueduct of Fallopius or outside of this canal. If the lesion be external, there is simple paralysis of the facial muscles. If it be internal, there is also a diminished activity of circulation and secretion in the submaxillary gland.

Another symptom sometimes observed in deep-seated lesions of the facial nerve, which is also dependent on injury of the chorda tympani, is a diminution or disturbance of the *sense of taste* in the tip and surface of the tongue. In this affection, the taste is not absolutely abolished, but is diminished in acuteness, and especially in promptitude. In a person presenting this difficulty, or in an animal after division of the chorda tympani, if a bitter substance be placed alternately upon the two sides of the tongue, it is perceived almost immediately upon the sound side, but only after a considerable interval on the side of the

[1] Système Nerveux. Paris, 1858, tome ii. pp. 150–157. Liquides de l'Organisme Paris, 1859, tome i. pp. 310–315.

paralysis. Various explanations are given to account for these phenomena. By some writers they are referred exclusively to the motor properties of the chorda tympani. If the fibres of this nerve which accompany the branches of the lingual in their peripheral distribution have an influence upon the circulation and secretion in the tongue similar to that which they exert in the submaxillary gland, it is plain that when these actions are depressed by section of the chorda tympani, the sense of taste may be diminished in the corresponding parts as an indirect result of its paralysis. Others, on the contrary, attribute this effect to sensitive fibres in the chorda tympani, which convey the impressions of sapid substances directly from without inward, and which, of course, cease their action when the nerve is divided. The indications obtained by experiment on this point are as yet too obscure to allow of a decisive opinion. The precise manner in which the chorda tympani takes a share in the exercise of the sense of taste is more or less a matter of uncertainty. But there is no question that its paralysis interferes, to an appreciable degree, with this sense; and an alteration of the taste, accompanying facial paralysis upon the same side, is a symptom which fixes the location of the nervous lesion at some point inside the stylomastoid foramen.

Eighth Pair. The Auditory.

On the posterior surface of the medulla oblongata, a little behind the widest part of the fourth ventricle, a number of white striations run from the neighborhood of the median line, transversely outward, toward the posterior edge of the peduncles of the cerebellum. These striations, which are sometimes exceedingly distinct, represent the commencement of the roots of the auditory nerve. The nucleus from which they originate is a mass of gray substance situated directly beneath them, containing nerve cells of various form and size, some of which belong to the smaller variety, while some of them, according to Dean, are among the largest of those met with in the nervous system. The gray matter of the nucleus, at its lateral portion, extends outward and upward toward the white substance of the cerebellum, with which it is connected by numerous bundles of radiating fibres.

The fibres originating from this ganglion partly run directly outward in a superficial course, forming the white striations visible at this point, and, uniting with each other, curve round the posterior border of the peduncles of the cerebellum to reach the lateral surface of the medulla at the lower edge of the pons Varolii. Some of them follow a deeper course, passing obliquely through the substance of the medulla outward and downward to the same point. These fibres, united with each other, form the posterior root of the auditory nerve.

The anterior root consists of fibres which are traced backward from their point of emergence, partly to the floor of the fourth ventricle, but also in great measure, according to Clarke, Dean, and Henle, into the white substance of the cerebellum, where they mingle with fibres coming

from the interior of this organ. The main anatomical peculiarity, therefore, which distinguishes the central origin of the auditory from that of the other cranial nerves, is its abundant and direct connection with the substance of the cerebellum

The auditory nerve, formed by the union of these two bundles of root fibres, emerges from the lateral surface of the medulla oblongata, at the inferior edge of the pons Varolii, and immediately outside the facial nerve. In company with the facial it then passes forward and outward, enters the internal auditory meatus, penetrates through the perforations at the bottom of this canal, and terminates in the nervous expansions of the internal ear.

Physiological Properties of the Auditory Nerve.—The auditory nerve is evidently a nerve of special sense, and serves to communicate to the brain the impression of sonorous vibrations. In the experiments of Magendie upon dogs and rabbits, the auditory nerve, when exposed in the cranial cavity, was found to be insensible to the severest mechanical irritation, although the roots of the fifth pair exhibited at the same time an acute sensibility. Its exclusive distribution to the internal ear, for which it forms the only nervous connection with the brain, leaves no doubt that its function is that of transmitting to the central organ the nervous influences which produce the sensation of sound.

Behind the situation of the auditory there commences a special division of the cranial nerves, which differ in great measure from the preceding. All the foregoing nerves, excepting those of special sense, are either distinctly motor or have a highly developed general sensibility; they are distributed to the integument and to muscles which are concerned in the execution of voluntary movements; and they are all associated in the production of nervous action in the various regions of the face.

The second division of the cranial nerves, on the other hand, comprising the glossopharyngeal, the pneumogastric, and the spinal accessory, are distributed to the deeper parts about the commencement of the digestive and respiratory passages, where the general sensibility is comparatively deficient, and the movements are, for the most part, involuntary; and they exhibit phenomena which have more especially the character of reflex actions. Externally, they show a marked similarity of anatomical arrangement, originating one behind the other, in a continuous line, along the lateral furrow of the medulla oblongata and the side of the spinal cord, each by a series of separate filaments; and in such juxtaposition that it is in some instances difficult to say, from external inspection, where the root fibres of one terminate, and those of the other begin. The two sensitive nerves belonging to this group, namely, the glossopharyngeal and the pneumogastric, have their source in two nuclei which are continuous with each other at the posterior surface of the medulla oblongata; and, according to the observa-

tions of Dean, in the medulla of the sheep, the transition between the pneumogastric and glossopharyngeal roots or nuclei is so gradual that it is impossible to point out any exact line of demarcation. Each of these nerves has upon its trunk a distinct ganglion, situated within its point of emergence from the cranium. The motor portion of the group, or the spinal accessory, originates from a special nucleus of its own, and sends branches of communication to both the other nerves. While the three nerves of this group, therefore, can hardly be regarded as a single pair, they have nevertheless a close mutual relation both in anatomical arrangement and in their physiological properties.

Ninth Pair. The Glossopharyngeal.

The fibres of the glossopharyngeal nerve originate from a nucleus situated a little behind and below that of the auditory, and near the outer border of the fasciculus teres, by which it is separated from the median line. This nucleus is continuous posteriorly with that of the pneumogastric nerve, which projects above it on the floor of the fourth ventricle (Fig. 168, Ngl, Nv). The nerve fibres, after leaving the nucleus, pass downward and outward through the substance of the medulla, and emerge from its lateral surface, next behind the auditory nerve, in a series of five or six filaments which soon afterward unite into a single cord. The nerve then passes into and through the jugular foramen, in company with its associated nerves, the pneumogastric and spinal accessory. While passing through this opening in the skull, it presents a ganglionic enlargement, similar to those of the posterior spinal nerve roots, and known as the *petrosal ganglion*, from its occupying a shallow depression in the petrous portion of the temporal bone. At the situation of the petrosal ganglion it gives off a small branch, the "nerve of Jacobson," which is distributed to the mucous membrane of the tympanum and Eustachian tube, and sends a filament of communication to the otic ganglion of the sympathetic system. The trunk of the glossopharyngeal nerve then passes downward and forward, receiving branches of communication from both the facial and the pneumogastric nerves, after which it separates into two main divisions, one of which is destined for the tongue, the other for the pharynx; a double distribution, to which the nerve owes its name. The portion passing to the tongue is distributed to the mucous membrane of the posterior third of this organ, namely, to that portion situated behind the V-shaped row of circumvallate papillæ, and to these papillæ; it also supplies filaments to the tonsils and to the mucous membrane of the pillars of the fauces and of the soft palate. The remaining portion of the nerve is distributed to the mucous membrane of the pharynx and certain of the adjacent muscles, namely, the digastric and stylopharyngeal muscles, by union with a branch of the facial to the styloglossal muscle, and by union

[1] Gray Substance of the Medulla Oblongata and Trapezium. Washington, 1864, p. 30.

with branches of the pneumogastric to the mucous membrane and the superior and middle constrictors of the pharynx. The muscles, accordingly, to which this nerve is directly or indirectly distributed are those by which the tongue is drawn backward (styloglossal), the larynx and pharynx elevated (digastric and stylopharyngeal), and the upper part of the pharynx contracted (superior and middle constrictors); that is, those concerned in the act of deglutition.

Physiological Properties of the Glossopharyngeal.—The glossopharyngeal nerve is evidently for the most part a nerve of sensibility. Its origin from the tract of gray matter in the medulla oblongata corresponding to the posterior horns of gray matter in the spinal cord, the distinct ganglion located upon its trunk in the jugular foramen, and the fact that it is mainly distributed to the mucous membranes of the tongue and pharynx, all indicate its resemblance in anatomical arrangement to other well known sensitive nerves or nerve roots. The result of direct experiment corroborates this view. Longet, in irritating the glossopharyngeal nerve within the cranium, was never able to produce muscular contraction; and although Chauveau, in experimenting upon this nerve in the same situation in recently killed animals, saw its galvanization followed by contraction of the upper part of the pharynx, the effect may have been due to reflex action, since the nerve was still in connection with the medulla oblongata. This conclusion is rendered certain by the investigations of Reid,[1] who found that irritation of the glossopharyngeal nerve produced movements of the throat and lower part of the face; but that these movements were, in a great measure, reflex and not direct, since they were also produced after the nerve had been divided, by applying the irritation to its cranial extremity. Its sensibility to mechanical or galvanic irritation, however, appears to be of a low grade, as compared with that of the trigeminal nerve. While some observers (Reid) found its irritation in the living animal, outside the jugular foramen, give rise to evident signs of pain, others (Panizza) have failed to see any indications of suffering from this cause; and others still (Longet) speak of the signs of pain, thus produced, in a more or less uncertain manner. This variation in the observed results is sufficient to show the inferior capacity of the glossopharyngeal nerve for the receipt of painful impressions; since no experimenter has ever doubted the acute sensibility of the fifth pair.

But notwithstanding the comparative deficiency of the nerve itself, and the parts to which it is distributed, in ordinary sensibility, it serves to transmit sensitive impressions of a special character, which are connected with two different but associated functions, namely: 1. The sense of taste, and, 2. The reflex act of deglutition.

Connection with the Sense of Taste.—The power of perceiving sensations of taste exists not only in the anterior portion of the tongue which

[1] Todd's Cyclopædia of Anatomy and Physiology. Article, *Glossopharyngeal Nerve.*

contains filaments derived from the lingual branch of the fifth pair, but also at the base of the organ, throughout its posterior third, and in the mucous membrane of the arches of the palate, which are supplied only by the fibres of the glossopharyngeal. The difference between these two regions is that while that supplied by the fifth pair possesses tactile sensibility of a high grade in addition to that of taste, in the posterior region the general sensibility is less acute than the special sensibility to impressions of taste. The appreciation of savors is provided for by both the lingual and glossopharyngeal nerves, each in its separate department of the oral cavity. The sense of taste accordingly, in the experiments of Reid, was never completely abolished by division of either one of these nerves. For its complete suspension, both of them must be destroyed on both sides. The method adopted by Longet for examining the condition of the taste in dogs, before and after division of the glossopharyngeal nerves, was to place upon the base of the tongue a few drops of a concentrated solution of colocynth. Although this always produced in the animals, while in their natural condition, manifest signs of disgust, it had no such effect, as a general rule, after section of the glossopharyngeal nerves on both sides, provided the solution were applied only to the posterior part of the tongue and the pharynx; while if even a minute quantity came in contact with the tip or edges of the tongue it caused brisk movements of the jaws with all the indications of a sense of repugnance. While in the anterior and more movable parts of the tongue, accordingly, the sensations of taste are appreciated, during the process of mastication, by the filaments of the lingual nerve which are distributed there, the glossopharyngeal is the nerve of taste for the posterior part of the organ. It is called into activity after mastication is accomplished and at the moment when the food is carried backward and compressed by the base of the tongue, the pillars of the fauces, and the walls of the pharynx.

Connection with the Reflex Act of Deglutition.—In the fauces and pharynx, the glossopharyngeal nerve also possesses a peculiar sensibility to certain impressions, which excite at once the muscles of the neighboring parts and bring into play the complicated mechanism of deglutition. This consists in drawing backward and upward the base of the tongue, thus bringing the masticated food into and through the isthmus of the fauces. The muscles of the pillars of the fauces (palato-glossal and palato-pharyngeal) afterward contract and close the opening of the isthmus, while the soft palate is drawn backward and extended across the upper end of the pharynx, thus shutting off its communication with the posterior nares; and the contraction of the constrictor muscles of the pharynx then forces its contents downward into the beginning of the œsophagus. This process is an involuntary one. Both the contraction of the special muscles, and their regular co-ordination in the necessary series of successive movements, are actions which do not depend on the exercise of the will, but which take place even in a state of unconsciousness under the stimulus supplied by contact of food or liquids with the

inner surface of the fauces and pharynx. This contact produces an impression which is conveyed by the glossopharyngeal nerve inward to the medulla oblongata, whence it is reflected outward in the form of a motor impulse. The sensibility which, by the contact of masticated food or nutritious liquids, thus produces the movements of swallowing, if subjected to the influence of nauseous or irritating substances, will cause an inverted muscular reaction, equally involuntary in character.

Natural stimulants, therefore, applied to the mucous membrane of the pharynx, excite deglutition; unnatural stimulants excite vomiting. If the finger be introduced into the fauces and pharynx, or if the mucous membrane of these parts be irritated by tickling with the end of a feather, the sensation of nausea, conveyed through the glossopharyngeal nerve, is sometimes so great as to produce immediate vomiting. This method may be employed in cases of poisoning, when it is desirable to excite vomiting rapidly, and when emetic medicines are not at hand.

Motor Properties of the Glossopharyngeal.—Although this nerve is shown, by the result of observation, to be exclusively sensitive at its origin, it is found, if examined outside the cavity of the cranium, to possess motor properties. In the experiments of Herbert Mayo upon the ass, confirmed by those of Longet on the horse and the dog, irritation of this nerve in the neck produced contraction in the stylopharyngeal muscles and in the upper part of the pharynx. These movements were not the result of reflex action, but were excited through the nerve from within outward; since, in the experiments of Longet, they were called out after the nerve had been divided, by applying the irritation to its peripheral extremity.

The glossopharyngeal, therefore, after its exit from the jugular foramen, is a mixed nerve. In addition to its own original sensitive filaments, it has received a branch of communication from the facial which is undoubtedly of a motor character, and also a branch from the pneumogastric. The pneumogastric branch is also regarded, on anatomical grounds, as really made up, wholly or in part, of motor fibres derived from the spinal accessory, through its anastomosis with the pneumogastric. According to Cruveilhier, it sometimes comes directly and exclusively from the anastomotic branch of the spinal accessory; sometimes partly from this and partly from the pneumogastric itself. The results obtained by experiment also indicate a double source for the motor fibres which join the glossopharyngeal before its exit from the skull. If these fibres were derived exclusively from the facial or exclusively from the spinal accessory, the division or destruction of one or the other of these nerves above its communicating branch would abolish entirely the motor power of the glossopharyngeal. But the experiments of Bernard upon rabbits, in which the facial nerve was divided in the aqueduct of Fallopius, and those of Bernard and Longet on cats and rabbits, in which the spinal accessory was destroyed on both sides, show that the process of deglutition, though more or less retarded, is not abolished by either of these operations.

Beside the anastomotic branches received by the glossopharyngeal, near its origin, from the facial and the spinal accessory, it also has communication with both these nerves near its peripheral distribution. It is joined by a branch of the facial, which accompanies it to the stylo-glossal muscle, and perhaps also to the pillars of the fauces; and, according to Cruveilhier, a branch derived from the spinal accessory takes part in the formation of the pharyngeal plexus which supplies the upper constrictor muscles of the pharynx. The process of deglutition, therefore, is excited at its commencement by sensitive impressions conveyed through the glossopharyngeal nerve; but its movements are executed by a reflex impulse transmitted through the motor fibres of several distinct branches of communication.

Tenth Pair. The Pneumogastric.

The pneumogastric nerve, remarkable for its varied and extensive course and the distribution of its fibres to a number of different localities, has received its name from the two most important organs in which it terminates, the lungs and stomach. It arises from the side of the medulla oblongata by a series of from ten to fifteen separate filaments, arranged in a linear series, continuously with those of the glossopharyngeal. The nucleus from which these fibres take their origin is an extended tract of gray matter running in a longitudinal direction along the posterior surface of the medulla oblongata, just outside the lower extremity of the fasciculus teres. This collection of gray matter (Fig. 168, N*v*) which is uncovered by the divergence of the posterior columns of the cord, and is thus exposed to view on the floor of the fourth ventricle, is known as the *ala cinerea.* At its anterior extremity it covers, and is continuous with, the nucleus of the preceding nerve, the glossopharyngeal; and at its posterior extremity it joins that of the following nerve, the spinal accessory. From its deep surface it gives out the fibres of origin of the pneumogastric nerve, which run downward and outward through the substance of the medulla, and emerge, as above mentioned, in a series of filaments from its lateral surface.

The filaments of the pneumogastric, after leaving the side of the medulla oblongata, unite into a single trunk which passes out of the cranium, in company with the glossopharyngeal and the spinal accessory, by the jugular foramen (Fig. 179). Here it presents upon its trunk a ganglionic swelling, known as the "jugular ganglion." At or immediately beyond the situation of the ganglion, the nerve is joined by an important motor branch of communication from the spinal accessory; and it afterward receives filaments from four other sources; namely, the facial, the hypoglossal, and the anterior branches of the first and second cervical nerves.

While passing down the neck the pneumogastric nerve takes part, by an anastomotic branch, in the formation of the pharyngeal plexus. Its first important branch of distribution is the *superior laryngeal nerve*,

which runs downward and forward, penetrates the larynx by an opening in the side of the thyro-hyoid membrane, and is distributed to the mucous membrane covering the epiglottis and lining the interior of the laryngeal cavity. This is the main portion of the nerve, and it is sensitive in character; providing for the peculiar sensibility of the glottis and epiglottis and for that of the inner surface of the larynx in general. The nerve gives off, however, a small muscular branch which terminates in the inferior constrictor of the pharynx and in the crico-thyroid muscle of the larynx. It also supplies several filaments, which unite with others coming from the great sympathetic, to form the *laryngeal plexus;* and by this plexus the superior laryngeal branch of the pneumogastric furnishes filaments to the upper cardiac nerves of the cervical portion of the sympathetic. Other filaments pass off from the trunk of the pneumogastric while passing down the neck, which also join the cardiac branches of the sympathetic, and which in some instances, according to Cruveilhier, pass directly downward, to unite with the cardiac plexus beneath the concavity of the arch of the aorta.

The next branch is the *inferior laryngeal nerve*, which separates from the trunk of the pneumogastric after entering the cavity of the chest, curves round the subclavian artery on the right side and the arch of the aorta on the left, and ascends, in the groove between the trachea and œsophagus, to the larynx, giving off branches to the œsophagus and the inferior constrictor muscle of the pharynx. In the larynx it is distributed to all the muscles of this organ, excepting the crico-thyroid, which is supplied by the superior laryngeal. The larynx is therefore supplied by two different branches of the pneumogastric nerve, which are mainly distinct from each other in their properties and functions. The superior laryngeal branch is for the most part a sensitive nerve, sup-

Fig. 179.

Origin and Course of the Glossopharyngeal, Pneumogastric, and Spinal Accessory Nerves.—1. Facial nerve. 2. Glossopharyngeal. 3. Pneumogastric. 4. Spinal accessory. 5. Hypoglossal. 6. External (muscular) branch of the spinal accessory. 7. Superior laryngeal branch of the pneumogastric. 8. Pharyngeal plexus. 9. Laryngeal plexus and upper cardiac branches of the pneumogastric. 10. Tympanic plexus, from a branch of the glossopharyngeal. (Hirschfeld.)

plying the mucous membrane of the larynx; the inferior laryngeal branch is a motor nerve, and is essential to the activity of nearly all the muscles of the organ.

After entering the cavity of the chest, the most important dependency of the pneumogastric nerve is the *pulmonary plexus*, formed by the separation of the nerve into a considerable number of inosculating branches which send their terminal filaments along the course of the bronchi and their subdivisions, to the ultimate bronchi and lobules of the lungs. In the inferior portion of the chest, the inosculating filaments on both sides surround the œsophagus with the *œsophageal plexus*, from which fibres are supplied to the mucous membrane and muscular coat of this organ.

The two pneumogastric nerves, after being reconstructed by the union of their branches below the pulmonary plexus, penetrate the cavity of the abdomen and spread out in two sets of *gastric branches*, which supply the mucous membrane and muscular coat of the stomach. Those belonging to the left pneumogastric nerve supply the anterior wall of the organ, and, extending toward the right as far as the pylorus, send a continuation of nervous filaments to the transverse fissure of the *liver*, into which they penetrate, together with those of the hepatic plexus of the sympathetic; those belonging to the right pneumogastric send filaments to the posterior wall of the stomach, and finally communicate with the solar plexus of the sympathetic.

The pneumogastric nerve, therefore, is distributed, by its various branches, to the mucous membranes and muscular apparatus of the passages by which air and food are introduced into the interior of the body. It also forms connection at several points with branches of the great sympathetic, and, through it, sends fibres to the central organ of the circulation, and to the radiating sympathetic plexuses of the abdominal organs.

Physiological Properties of the Pneumogastric.—According to the results obtained by Longet, the pneumogastric is, at its origin, exclusively a sensitive nerve. Galvanic irritation applied to the nerve roots, carefully separated from the medulla and from adjacent filaments, was not found to produce any muscular contractions; but when applied to the trunk of the nerve at a lower level, muscular contractions were readily excited. At this situation the nerve already contains motor fibres derived from inosculation with the spinal accessory, the facial and the hypoglossal, and from the loop of communication between the two upper cervical nerves. In its trunk, accordingly, it has the characters of a mixed nerve, and is capable of providing both for movement and sensibility in the organs to which it is distributed.

The sensibility of the pneumogastric nerve, however, to mechanical irritation and to painful impressions, is but slightly marked, as shown by the experience of all observers. It may frequently be divided in the middle of the neck in the living, unetherized animal, without any sign of pain being manifested; and this want of reaction is at times so

complete as to indicate an entire absence of ordinary sensibility. This does not seem to be invariably the case; but although Bernard has found in some instances a well-marked sensibility in this nerve, and in others only a very indistinct one, it is not possible to say with certainty upon what special conditions the difference depends. As a general rule, the pneumogastric nerve is decidedly deficient in that kind of sensibility which produces pain; and we know that the organs to which it is distributed have but little appreciation of tactile impressions. Nevertheless, there is abundant evidence that this nerve is endowed, in its various divisions, with sensibility of a peculiar kind, and one which is of the highest importance for the due performance of the vital functions.

Connection with the movements of Respiration.—The most important endowment of the pneumogastric nerve is undoubtedly that by which it is connected with the reflex movements of expansion and collapse of the chest in respiration. Its influence in this respect is at once made evident by the results which follow the division of both nerves in their course through the neck. This may be readily done in adult dogs by etherizing the animal and exposing the nerves in the middle of the neck during the continuance of insensibility. After the etherization has passed off, and the circulation and respiration are restored to a quiescent condition, both nerves may be simultaneously divided, and the effects of the operation observed.

After the nerves have been divided, and the slight disturbance which immediately follows their section has subsided, the most striking change produced in the condition of the animal is a *diminished frequency in the movements of respiration.* The respirations sometimes fall at once to ten or fifteen per minute, becoming, in an hour or two, still further reduced. Respiration is performed easily and quietly; and the animal, if undisturbed, remains usually crouched in a corner, without any special sign of discomfort. If he be aroused and compelled to move, the frequency of respiration is temporarily augmented; but as soon as he is again quiet, it returns to its former standard. By the second or third day the respirations are often reduced to five, four, or even three per minute; when the animal usually appears very sluggish, and is roused with difficulty from his inactive condition. Respiration is also performed in a peculiar manner. The movement of inspiration is slow, easy, and silent, occupying several seconds in its accomplishment; while that of expiration is sudden and audible, and is accompanied by a well marked effort, which has, to some extent, a convulsive character. The intercostal spaces sink inward during the lifting of the ribs; and the whole movement of respiration has an appearance of insufficiency, as if the lungs were not thoroughly filled with air. This is undoubtedly owing to a peculiar alteration in the pulmonary texture, which has by this time already commenced.

Death takes place from one to six days after the operation, according to the age and strength of the animal. The only marked symptoms which accompany it are a steady failure of the respiration, with increas-

ing sluggishness. There are no convulsions, nor any evidences of pain. After death the lungs are found in a peculiar state of solidification. They are not swollen, but rather appear smaller than natural. They are of a dark purple color, leathery, and resisting to the touch, destitute of crepitation, and infiltrated with blood. Pieces of the lung cut out sink in water. The pleural surfaces, at the same time, are bright and polished, and their cavity contains no effusion or exudation. The lungs are simply engorged with blood, and, to a greater or less extent, empty of air; their tissue having undergone no other alteration.

These phenomena point to the pneumogastric nerves as the main channels through which the stimulus which excites the movements of respiration is conveyed inward to the medulla oblongata. Respiration is a reflex act, consisting, like other nervous manifestations of a similar character, of two different elements; namely, first, an impression conveyed from without inward by a sensitive nerve to the appropriate nervous centre; and, secondly, of a motor impulse transmitted thence through motor nerves to the muscular apparatus. But by dividing the pneumogastric nerves in the neck, neither the intercostal muscles nor the diaphragm are paralyzed. The muscular apparatus which effects the expansion of the lungs remains untouched, and yet the movements of respiration become gradually slower until they cease altogether. At the same time the disturbance of respiration, under these circumstances, although sufficient to produce death after a short interval, is not accompanied by any apparent sense of suffocation. The retarded breathing, and the consequent imperfect aeration of the blood, are not felt by the animal, and he accordingly makes no attempt to compensate for them by voluntary effort.

In dividing the pneumogastric nerves, therefore, it is not the motor, but the sensitive element in the reflex act of respiration which is interfered with. The experiments of Waller and Prevost[1] show conclusively that this is the part performed by the nerves in question. In these experiments the pneumogastric nerve was exposed in the living dog, and divided in its course down the neck; after which, galvanization of its central extremity produced a succession of forcible inspirations and expirations, expelling the air through the trachea with an audible sound. The respiratory impulse, therefore, is propagated through the pneumogastric nerve in a centripetal, not in a centrifugal direction. The impression which normally originates in the lungs, and is thence conveyed through these nerves to the medulla oblongata, produces in the nervous centre, though unperceived as a conscious sensation, the stimulus which calls into activity the muscles of respiration. If this impression be not at once satisfied by filling the lungs with air, it increases in intensity; and if the breath be voluntarily suspended or forcibly obstructed, the impression soon becomes perceptible as a sensation of distress, or "demand for breath," which reacts upon the entire system.

[1] Archives de Physiologie normale et pathologique. Paris, 1870, p. 190.

On the other hand, if the pneumogastric nerves be cut off, the customary impression is no longer conveyed from the lungs to the medulla, and the movements of respiration are consequently retarded. The imperfect aeration of the blood thus induced reacts in turn upon the medulla, as well as upon the other nervous centres, diminishing its sensibility, and rendering it less able to respond to impressions of any kind. Thus the difficulty, which consists in a want of the nervous reaction necessary for respiration, increases from hour to hour, the breathing becomes constantly more imperfect and sluggish, and at last ceases altogether. The alteration in the tissue of the lungs, their engorgement and solidification, add to the difficulty in aeration of the blood, and probably have, at last, a considerable share in producing the fatal result.

It is evident, however, that the pneumogastric nerves, although the principal means for conveying to the medulla the stimulus for respiration, are not the only ones. If they were so, respiration would stop instantly after section of these nerves, as it does after destruction of the medulla itself. The lungs are, no doubt, especially sensitive to the want of oxygen and accumulation of carbonic acid in the blood; and the nervous impression thus produced is accordingly first felt in them. There is reason to believe that all the vascular organs are more or less capable of originating this impression, and that all the sensitive nerves are capable, to some extent, of transmitting it. Although the first disagreeable sensation, on holding the breath, makes itself felt in the lungs, yet if we persist in suspending respiration, the feeling of discomfort soon spreads to other parts; and at last, when the accumulation of carbonic acid has become excessive, all parts of the body are pervaded by a general feeling of distress. It is easy, therefore, to understand why respiration should be retarded, after section of the pneumogastrics, since the chief source of the stimulus to respiration is cut off; but the movements still go on, though more slowly than before, because the other sensitive nerves, which continue to act, are in some measure capable of conveying a similar impression.

In order that the movements of respiration should go on with the requisite frequency to maintain the aeration of the blood, it is necessary that the pneumogastric nerves, which are especially endowed with this kind of sensibility, retain their integrity as nervous conductors between the lungs and the medulla oblongata. In this function, they act altogether as sensitive nerves; while the muscles of respiration receive their reflex motor stimulus by way of the spinal nerves.

Connection with the Respiratory Movements of the Glottis.—The respiratory movements of the glottis, already described in a former chapter (p. 277) are essential parts of the mechanism of respiration. They consist in the active opening of the glottis in inspiration, followed by its partial collapse at the time of expiration. The opening of the glottis, which is requisite for the free admission of air into the trachea, is effected by the action of the posterior crico-arytenoid muscles. These muscles, in contracting, rotate the arytenoid cartilages outward, and

thus separate the vocal chords from each other and largely increase the transverse diameter of the orifice of the glottis. When they relax at the time of expiration, the arytenoid cartilages return to their former position, and the opening of the glottis is again narrowed by the passive approximation of the vocal chords. As the movements of expansion are accomplished by the action of the laryngeal muscles, they depend upon the influence of the pneumogastric nerve and its inferior laryngeal branch.

Both the movements of the glottis in respiration and their dependence upon nervous influence may be seen in the dog by means of an operation which consists in making a dissection along the side of the neck, in such a way as to expose the pharynx and a considerable portion of the œsophagus. The superior laryngeal nerve on that side is necessarily cut across, but the inferior laryngeal, as well as the trunk of the pneumogastric, are left uninjured. By a longitudinal incision through the pharynx and œsophagus, the upper and posterior surfaces of the larynx are then exposed, and, notwithstanding the previous division of the superior laryngeal nerve, the alternate movements of expansion and collapse of the glottis are seen going on in their natural order, and keeping pace with the corresponding respiratory movements of the chest. If now the inferior laryngeal nerve be divided upon either the right or the left side, the vocal chord of that side becomes motionless, while that of the opposite side continues to move as before. If the remaining laryngeal nerve be divided, all movements of expansion in the vocal chords instantly cease; and the same effect is produced by section of both pneumogastric nerves in the middle of the neck, since the inferior laryngeals are given off as branches below that point.

If the section of both pneumogastric nerves, or of their inferior laryngeal branches, be made simultaneously under these circumstances while the breathing is tolerably rapid, the injurious effect of laryngeal paralysis upon respiration at once becomes manifest. Both vocal chords being then deprived of the active control of their muscles, the borders of the rima glottidis are left in a condition of passive flexibility. They have not only lost the power of separating from each other and thus opening the glottis at the time of inspiration, but they are also drawn downward and inward by the current of air passing into the trachea, and thus, like a double membranous valve, they occlude more or less completely the orifice of the glottis, and offer a physical obstacle to the free entrance of the air. In very young animals, where there is but little rigidity of the laryngeal cartilages, the occlusion of the glottis thus produced after section of the inferior laryngeal nerves, may be so complete as to produce immediate death by suffocation; in adult animals the occlusion is only partial, but is still sufficient to diminish perceptibly the capacity of respiration.

The natural movements of the glottis in breathing are therefore reversed after section of the inferior laryngeal nerves. Before this operation, in the normal condition, the glottis is opened at inspiration

and collapses in expiration; after the section of the nerves, it is narrowed in inspiration and passively opened in expiration by the forcible expulsion of the air. The effects thus produced on the glottis, by division of the inferior laryngeal nerves, are the same with those which take place in the nostrils after division of the facial nerves. Both these sets of movements are connected with the mechanism of respiration, and both are influenced in a similar manner by division of their motor nerves.

As the laryngeal muscles are necessarily paralyzed by division of the pneumogastric nerves in the middle of the neck, the effects of this muscular paralysis are necessarily added to those which result from interruption of the sensitive function of the pneumogastric branches in the lungs. In very young animals, as mentioned above, the effects due simply to laryngeal paralysis are more marked than in adults; and in order to determine the extent of its influence upon the lungs we have performed a comparative experiment, in the following manner. Two pups were taken belonging to the same litter, and of the same size and vigor, about two weeks old. In one of them (No. 1) a section was made of both pneumogastric nerves in the middle of the neck; in the other (No. 2), the inferior laryngeal nerves only were divided, the pneumogastrics being left untouched. In No. 1, therefore, the natural stimulus to respiration was diminished at the same time that the muscles of the larynx were paralyzed; in No. 2, there was laryngeal paralysis alone, the sensibility to the demand for respiration remaining the same. For the first few seconds after the operation there was but little difference in the condition of the two animals, the laryngeal symptoms being most prominent in both. There was the same obstruction at the glottis owing to paralysis of the laryngeal muscles, the same difficulty of inspiration, and the same frothing at the mouth. Very soon, however, in No. 1, the respiratory movements became quiescent, and at the same time much reduced in frequency, falling to ten, eight, and five respirations per minute, as usual after section of the pneumogastrics; while in No. 2 the respiration continued frequent as well as laborious, and the general signs of agitation and discomfort were kept up for one or two hours, after which there followed diminished excitability of the nervous centres, and the animal became exhausted, cool, and partially insensible, like the other. They both died between thirty and forty hours after the operation. On *post-mortem* inspection it was found that congestion and solidification of the lungs existed to a similar extent in each instance; and the only appreciable difference between the two bodies was that in No. 1 the blood was coagulated, and the abdominal organs natural, while in No. 2 the blood was fluid and the abdominal organs congested. The alteration in the tissue of the lungs, therefore, after the pneumogastric nerves have been divided, is not a direct effect, produced by cutting off the influence of these nerves upon the pulmonary tissue, but results indirectly from the diminished activity of respiration and imperfect aeration of the blood.

Protection of the Glottis from the Intrusion of Foreign Substances.—The influence of the pneumogastric nerve in the larynx is not confined to its motor action upon the muscles; it also supplies, by its superior laryngeal branch, a peculiar sensibility to the mucous membrane of these parts, which is essential for the protection of the respiratory passages. In the first place, it stands as a sort of guard, or sentinel, at the entrance of the larynx, to prevent the intrusion of foreign substances. If a crumb of bread fall within the aryteno-epiglottidean folds, or on the edges of the vocal chords, or upon the posterior surface of the epiglottis, the sensibility of the parts excites an expulsive cough, by which the foreign body is dislodged. The impression received and conveyed inward by the sensitive fibres of the superior laryngeal nerve, is reflected upon the expiratory muscles of the chest and abdomen, by which the movements of coughing are accomplished. Touching the above parts with the point of a needle, or pinching them with the blades of a forceps, will produce the same effect. This reaction is dependent on the sensibility of the laryngeal mucous membrane; and it can no longer be produced after section of the superior laryngeal branch of the pneumogastric nerve.

Connection with the Formation of the Voice.—In addition to its function in the mechanism of respiration, the larynx is also an organ for the production of vocal sounds. The formation of the voice can be studied in the lower animals by exposing the larynx and glottis in the manner described above, and in man by the use of the *laryngoscope;* that is, a small mirror held at a suitable angle at the back of the pharynx in such a way as to reflect a more or less complete view of the laryngeal orifice. The first important fact to be observed in this respect is that the voice is formed always in expiration, never in inspiration. It is the column of outgoing air which is set in vibration to produce a vocal sound, and which continues and modifies its resonance while passing through the pharynx, mouth, and nasal passages. Secondly, it requires an active tension and close approximation of the vocal chords, so that the orifice of the glottis is narrowed to a comparatively minute crevice. So long as the vocal chords preserve their relaxed condition during expiration, nothing is heard except the faint whisper of the air passing through the cavity of the larynx. When a vocal sound, however, is to be produced, the chords are suddenly made tense and applied closely to each other, thus diminishing considerably the diameter of the orifice; and the air, driven by forcible expiration through the glottis, in passing between the vibrating vocal chords, is itself thrown into vibrations which produce the sound required. The tone, pitch, and intensity of this sound vary with the conformation of the larynx, the degree of tension and approximation of the vocal chords, and the force of expiration. The narrower the opening of the glottis, and the greater the tension of the chords, the more acute the sound; while a wider opening and a less degree of tension produce a graver note. The quality of the sound is also modified by the length of the column of air included between the glottis and the mouth, the tense or relaxed condition of the walls of the

pharynx and fauces, and the state of dryness or moisture of the mucous membrane lining the passages.

The actual formation of the voice, or the production of sonorous vibrations, takes place, therefore, exclusively in the larynx; while articulation, or the division of the vocal sound into words and phrases by vowels and consonants, is accomplished by the aid of the lips, tongue, teeth, and palate. Consequently, division of the pneumogastric nerve or of its inferior laryngeal branch on both sides, by paralyzing the muscles of the larynx which serve to approximate and extend the vocal chords, produces among its other effects a loss of voice. Furthermore, as the two functions of vocalization and articulation are accomplished by distinct nervous and muscular actions, they may be deranged independently of each other, by injury or disease of different parts of the nervous system. That of articulation is regulated by the action of the facial and hypoglossal nerves; while vocalization is under the control of the pneumogastric.

Connection with Deglutition.—The reflex act of deglutition, which commences in the fauces and pharynx under the control of the glosso-pharyngeal nerve, is continued and completed by the lower portion of the pharynx and the tube of the œsophagus. These parts receive both their sensitive and motor filaments exclusively from the pneumogastric nerve, and it is under its influence that the food, once started upon its downward passage, is conducted by the peristaltic action of the œsophagus into the stomach.

The inferior constrictor muscle of the pharynx and the cervical portion of the œsophagus both receive filaments from the inferior laryngeal nerve; while the thoracic portion of the œsophagus is supplied entirely from the trunk of the pneumogastric. Some fibres are also sent to the inferior constrictor of the pharynx by the superior laryngeal nerve. Deglutition, therefore, becomes incomplete, as shown by the experiments of Bernard upon dogs, horses, and rabbits, by division of the pneumogastric nerves in the middle of the neck. The masticated food is still conveyed, by the action of the pharynx, from the fauces into the œsophagus; but here it accumulates, distending the inert walls of the paralyzed canal, and finding its way into the stomach only in small quantities and by the imperfect effect of compression from above. In the natural condition, the process of swallowing is a connected series of rapidly succeeding contractions, beginning at the fauces and ending at the cardiac orifice of the stomach. Each portion of the mucous membrane receives in turn a stimulus from the contact of the food, which is followed by excitement of the corresponding muscles; so that the alimentary mass is carried rapidly from above downward by an action which is reflex in character and independent of voluntary control. Section of the pneumogastric nerves destroys at once sensibility and motive power in the whole of the œsophagus, and thus interferes with complete deglutition.

There is no doubt that the sensitive nerves of the œsophageal mucous

membrane take their share in exciting the action of its muscular coat. The general sensibility of this canal, however, is very slight, as compared with the parts above, and is not usually sufficient to cause a perceptible impression from the food in the act of swallowing. Its muscular contraction takes place, as a general rule, without any effect on the consciousness; and it is only when the food is very cold or very hot, or when it contains pungent or irritating ingredients, that its passage through the œsophagus produces a distinct sensation.

It appears that the filaments of the superior laryngeal nerve, distributed about the anterior surface of the epiglottis and borders of the larynx, take an active part in exciting the movements of deglutition. In the experiments of Waller and Prevost on dogs and cats, galvanization of the superior laryngeal nerve produced, in many repeated trials, rhythmical movements of deglutition, consisting of contraction of the pharynx and elevation of the larynx, followed by peristaltic motion of the whole length of the œsophagus. All the sensitive fibres of the pneumogastric, therefore, distributed to the parts concerned in the act of swallowing, undoubtedly assist in exciting the necessary muscular contractions.

Protection of the Glottis in the act of Deglutition.—As the larynx communicates, by its superior orifice, directly with the cavity of the pharynx, and as all solids and liquids, in the act of swallowing, necessarily pass over its surface, portions of the food would be constantly liable to find their way through the rima glottidis into the respiratory passages, unless there were some provision against it. The epiglottis, which stands in front of the glottis in a nearly upright position, and which shuts down over its orifice like a cover when the base of the tongue is drawn back at the time of deglutition, might seem to be adapted to secure protection in this respect.

Experience shows, however, that the epiglottis is not essential for the safety of the glottis in deglutition. The entire organ may be cut off in dogs, as we have verified by repeated experiments, without any difficulty being afterward exhibited by the animal in swallowing either liquid or solid food. The epiglottis, furthermore, is an organ which exists only in mammalians, being absent in all the remaining classes of vertebrate animals. In birds especially, the orifice of the glottis can be readily seen on opening the beak, unprotected by anything similar to an epiglottis, and performing the alternate movements of expansion and collapse connected with respiration. Finally, the existence of the epiglottis in man does not prevent foreign substances from passing into the glottis whenever the other conditions of normal deglutition are suspended or disturbed. The protection of the glottis against the entrance of solid or liquid food does not depend upon a mechanical obstacle, but upon a definite association of nervous acts.

The first requisite for the act of swallowing is the *suspension of respiration.* This takes place, at the beginning of deglutition, by a nervous influence which it is difficult to describe, but which may be designated

as an "action of arrest." The same nervous impression which excites by reflex action the constrictors of the pharynx, suspends for a time the movements of inspiration. This effect is very perceptible in the ordinary act of swallowing, and was witnessed by Waller and Prevost in many of their experiments on this subject; galvanization of the central extremity of the superior laryngeal nerve causing immediate relaxation of the diaphragm, with stoppage of its movements.

The effect of the arrest of breathing upon the glottis is to prevent the customary opening of its orifice at the time of inspiration. As the respiratory movements of the glottis are coincident with those of the chest, and are excited and maintained by the same nervous influence, the impression which puts a stop to one suspends the other also. The glottis consequently, not being opened at the time the food enters the pharynx, its liability to admit any portion of the alimentary mass is much diminished by the mere fact of its passive condition. But this condition furthermore allows the rima glottidis to be completely closed by the contraction of the inferior constrictor of the pharynx, the most active muscle in the apparatus of deglutition; since the fibres of this muscle are attached laterally to the external surface and free borders of the thyroid cartilage, and thus compress the larynx on both sides at the moment the food is carried downward by their contraction. It is by this means alone that the glottis is protected in birds and in other animals where the epiglottis is wanting, and it is also the essential part of the same process in man and in mammalians.

The accident in which food or foreign substances sometimes gain access to the larynx is always produced by a sudden attempt at inspiration. This, which cannot take place during deglutition in the ordinary condition of the nervous system, may nevertheless be produced in many instances by an unexpected shock or excitement, which disturbs momentarily the harmonious co-ordination of the reflex actions. Any sudden impression produces in general, as its first effect, a spasmodic movement of inspiration; and if this take place while food is contained in the pharynx, a portion of it almost necessarily passes in, together with the current of air, through the widely open orifice of the glottis.

Connection with the Stomach and Stomach Digestion.—The effect produced upon the stomach and digestion by division of the pneumogastric nerve shows that its influence upon this organ is in the main similar to that which it exerts on the œsophagus; that is, it confers on its mucous membrane a certain sensibility to the presence of food, and provides for the peristaltic action of its muscular coat. After experimental section of both pneumogastric nerves in the region of the neck, the sensations of hunger and thirst remain; the animals often exhibiting a desire for food and drink, and sometimes taking it in considerable quantity, although little, if any, reaches the stomach, owing to the paralysis of the muscular walls of the œsophagus. In the experiments of Bernard on dogs, the secretion of gastric juice was suspended after this operation, and food introduced into the stomach through a gastric

fistula remained undigested. But Longet has found that if food be introduced under these circumstances in small quantity, it may cause the secretion of gastric juice, and may be finally digested and absorbed. These results indicate that the functions of secretion and digestion in the stomach are not immediately under the control of the pneumogastric nerve, but that they become deranged after its section and practically suspended, owing to the indirect influence of other causes.

On the other hand, the muscular contractions of the organ and the sensibility of its mucous membrane are both directly abolished by division of the pneumogastrics. According to the observations of Bernard, the finger, introduced into the cavity of the stomach through a gastric fistula in the dog, is compressed with considerable force by the walls of the organ; but this pressure disappears completely if the pneumogastric nerves be divided. The absence of muscular power in the paralyzed stomach is of itself sufficient to account for the failure of digestion when the influence of these nerves has been cut off. The peristaltic action of the organ is essential to the digestive process, in order to bring successive portions of the food in contact with its mucous membrane, and to cause the intimate admixture of the gastric juice with all parts of the alimentary mass. The natural movement and agitation of the food, by the action of the muscular coat, is no doubt, also, an important stimulus to the continued secretion of the gastric juice; and when it no longer takes place, the digestive fluid will necessarily be supplied in smaller quantity. It is evident, therefore, that the pneumogastric nerves supply to the walls of the stomach a certain amount of sensibility and a motor power, which are practically essential to the process of digestion.

Influence on the Action of the Heart.—The pneumogastric nerve, as already shown, gives off a number of filaments which are destined for the cardiac plexus, and ultimately for distribution in the substance of the heart. One or two of these filaments come from the superior laryngeal branch of the pneumogastric, and immediately join the upper cardiac nerve derived from the superior cervical ganglion of the sympathetic. Several others are furnished by the main trunk of the pneumogastric in the neck, which inosculate with each other and with the continuation of the upper cardiac nerve. The inferior laryngeal branch, in its reascending course through the lower part of the neck, supplies so many inosculating filaments to the same plexus of cardiac nerves that, according to Cruveilhier, it appears in some instances to be distributed in almost equal proportions to the larynx and to the heart. Finally other small branches are supplied by the pneumogastric in the cavity of the chest, which lose themselves at once in the cardiac plexus proper, beneath the arch of the aorta. All the filaments, accordingly, which are finally distributed to the heart through the cardiac plexus, originate from the sympathetic and the pneumogastric nerves; and the entire group is characterized by the frequent and intimate admixture of the fibres derived from these two sources. A considerable proportion of

the cardiac filaments are, therefore, made up of fibres originally belonging to the pneumogastric nerve.

The effect produced upon the heart's action by irritating the pneumogastric in the region of the neck is precisely the opposite to that usually caused by irritating the nerves going to a muscular organ. This effect may be seen by opening the chest, and exposing the heart to view, at the same time that the pneumogastric nerves are separated from their connections in the neck for a sufficient distance to apply to them the poles of a galvano-electric apparatus. In the cold-blooded animals, as the frog or the turtle, no other precaution is required; in the dog and other warm-blooded species, artificial respiration must be maintained by the nozzle of a bellows inserted in the trachea.

When a galvano-electric current of moderate strength is applied to the pneumogastric nerves prepared in this way, the cardiac pulsations are reduced in frequency; and if the current be increased in strength, the heart's action stops altogether, and remains suspended so long as the stimulus continues to be applied to the nerve. When the galvanization ceases, the cardiac pulsations recommence; and the same thing may be repeated for an indefinite number of successive trials.

There are two important facts to be noted in regard to these effects of irritating the pneumogastric:

1. When the heart ceases its movements under the galvanization of the nerves, its walls are not in a contracted condition, but in a state of relaxation. Neither are its cavities distended with blood; but the organ simply remains quiescent, lying at rest without any indication of muscular activity.

2. If the pneumogastric nerves be divided at their point of exposure in the middle of the neck, and if the central extremities be galvanized, no effect is produced upon the heart. But if the stimulus be applied to their peripheral extremities, the above phenomena are reproduced, the heart remaining flaccid so long as the galvanization is continued. The effect in question, therefore, is not due to reflex action, but to a direct influence conveyed through the pneumogastric filaments to the muscular substance of the heart. This conclusion is fully confirmed by the fact that a similar retardation or stoppage of the cardiac pulsations is caused in frogs and turtles by galvanization of the medulla oblongata itself, the pneumogastric nerves remaining entire; but if the nerves be previously divided, no such effect is produced. On the other hand, division of the pneumogastric nerves, or sudden destruction of the medulla oblongata, causes increased rapidity of the cardiac pulsations. Section of these nerves, accordingly, in the warm-blooded animals, produces opposite effects upon the respiration and the pulse, one being accelerated and the other retarded. According to Bernard, these effects, though opposite in direction, are produced in similar proportions; so that, if the respirations are diminished one-half, the cardiac pulsations are increased to double their former frequency. Thus when the influence of the pneumogastric nerve is cut off, the motions of the

heart increase in rapidity; when it is stimulated, they experience a retardation.

This influence, exerted upon the heart by the pneumogastric nerve, is of the peculiar kind known as the "action of arrest." Such a power certainly exists in the nervous system, though its nature is not easy of explanation. An instance of it has already been given in the fact, observed by Waller and Prevost, of suspension of the movements of the diaphragm by galvanizing the trunk of the superior laryngeal nerve. The natural stoppage of respiration in the act of swallowing, and the relaxation of the sphincters preliminary to the evacuation of the rectum and the bladder, are effected by nervous influences of a similar kind. There are evidently nervous fibres which transmit their stimulus directly to the muscles, and which, in this respect, belong to the category of motor nerves; but which, when called into activity, instead of exciting muscular contraction, serve to moderate or even suspend it. The most palpable instance of this mode of action is that of the pneumogastric nerves in their relation with the heart; but there is evidence that it occurs, in a more obscure manner, in various other parts of the nervous system.

Eleventh Pair. The Spinal Accessory.

This nerve, which has received its name from the singularity of its origin and subsequent course, consists of filaments which emerge from the side of the cervical portion of the spinal cord, from the level of the fourth or fifth cervical nerve upward (Fig. 179,$_4$). These filaments unite into a slender, rounded cord, which ascends in a vertical direction between the anterior and posterior roots of the cervical spinal nerves, gradually increasing in size from the addition of new root fibres from the spinal cord, to the level of the foramen magnum, where it enters the cranial cavity. Here it receives a new supply of accessory root fibres from the side of the medulla oblongata, which emerge in a continuous line with those of the pneumogastric nerve. The nerve trunk, thus constituted by the union of its spinal and its medullary roots, joins the pneumogastric and glossopharyngeal nerves in their passage through the jugular foramen.

The central origin of the root fibres of this nerve is a collection of nerve cells situated in the upper portion of the spinal cord and the commencement of the medulla oblongata, on the outer and posterior aspect of the anterior horn of gray matter. In the remainder of the medulla, this nucleus is situated farther backward, receding from front to rear with the rest of the gray matter in this part of the nervous centres. At its anterior extremity, it becomes continuous with the nucleus of the pneumogastric. From the gray matter of its nucleus, the fibres of the spinal accessory nerve curve downward and outward until they emerge, as above mentioned, in a series of bundles, from the lateral surface of the medulla.

While passing through the foramen lacerum, the spinal accessory

becomes adherent externally to the jugular ganglion of the pneumogastric, but without taking any part in its formation, except by furnishing one or two small filaments of communication. Immediately upon its exit from the foramen it divides into two main branches; namely, 1st, the *internal*, or anastomotic branch, which joins the trunk of the pneumogastric and becomes more or less intimately blended with it, and 2dly, the *external*, or muscular branch, which passes downward and outward and is distributed to the sterno-mastoid and trapezius muscles. According to many different observers (Bernard, Cruveilhier, Henle, Longet) the internal or anastomotic branch is made up of nerve fibres coming from the medulla oblongata; the external or muscular branch consists of those originating from the spinal cord.

The spinal accessory is without question a motor nerve. According to the experiments of Longet on dogs, its mechanical irritation in the cranial cavity does not give rise to signs of pain, and although Bernard found evidences of sensibility on galvanizing the uninjured nerve in the same situation, if it were divided and the irritation applied to its central extremity no indications of sensibility were manifest. On the other hand its fibres may be traced in great part directly to their termination in muscular tissues, and its division or evulsion induces effects which consist exclusively in loss of motive power.

The most complete method of experimenting upon the effects produced by destruction of this nerve is that first adopted by Bernard, namely, its evulsion. For this purpose, the muscular branch of the nerve is followed by dissection from without to its point of emergence from the jugular canal, where it separates from the anastomotic branch. The combined trunk is then seized between the blades of a forceps, and by a steady and continuous traction the whole of the nerve, with both its medullary and spinal roots, may be separated from their central attachments and extracted entire. By appropriate variations of the procedure, either the medullary portion with the anastomatic branch, or the cervical portion with the external branch, may be taken away separately, and the comparative effects of the two operations observed. But when the entire trunk is extracted as above, the source of the fibres destined both for anastomosis with the pneumogastric, and for the muscular branch of the nerve, is destroyed at the same time.

The most striking effects of this operation are due to paralysis of the internal or anastomotic branch. It is this branch which supplies to the pneumogastric nerve a large share of its motor fibres; and those especially which form the pharyngeal branch of the pneumogastric nerve, are shown by dissection to be derived from the anastomotic branch of the spinal accessory. According to Cruveilhier, the pharyngeal filament is sometimes given off exclusively from the anastomotic branch of the spinal accessory, sometimes partly from this branch and partly from the pneumogastric itself. Beyond the pharyngeal branch, the fibres of the pneumogastric nerve derived from the spinal accessory can no longer be followed with certainty by means of dissection; but the results of

experiment show that they are finally distributed, through the inferior laryngeal branch, to the muscles of the larynx, where they preside over its actions as a vocal organ.

After the spinal accessory nerve has been torn away on both sides in the manner above described, the most noticeable result is a *loss of power to produce vocal sounds.* The other movements of the larynx are not interfered with. Especially those of respiration go on in a natural manner. But the voice is completely lost, as much so as if the inferior laryngeal nerves, or the pneumogastric trunks themselves, had been divided. The difference between the two cases, however, is very important. Section of the pneumogastrics, or of their inferior laryngeal branches, paralyzes at once all the movements of the glottis, those of respiration as well as those of phonation; since these nerves contain all the motor fibres distributed to the larynx, except those of the crico-thyroid muscles. On the other hand, section or evulsion of the spinal accessory nerves paralyzes the movements of phonation alone, namely, those in which the vocal chords are approximated and the rima glottidis narrowed, while it leaves untouched the movements of respiration, in which the vocal chords are separated and the rima glottidis opened.

Thus the muscular apparatus of the larynx, which is destined to perform separately two distinct functions, is supplied with motor nerves from two different sources. Those which preside over the production of vocal sounds originate exclusively from the spinal accessory; those which excite the movements of respiration are derived from the other motor nerves (facial, hypoglossal, cervical) which also inosculate with the pneumogastrics.

The special function of the *external* or muscular branch of the spinal accessory nerve is not so fully understood. The sterno-mastoid and trapezius muscles, to which its fibres are distributed, also receive filaments from the cervical spinal nerves; and they still retain the power of motion after division or evulsion of the spinal accessory on both sides. The sterno-mastoid and trapezius muscles have no such peculiar and easily recognizable mode of action as that of the larynx in the formation of the voice; and consequently it has not been easy to distinguish with certainty what special movement of these muscles is paralyzed by division of the spinal accessory, and what remains unaffected. The most plausible conclusions are those derived by Bernard from continued observation of animals preserved for some time after the division of these nerves.

According to this explanation, the fibres of the external branch of the spinal accessory, like those of the internal branch, perform a function which is antagonistic to the movements of respiration. Respiration is naturally suspended in all steady and prolonged muscular efforts. In the acts of straining, lifting, pushing, and the like, respiration ceases, the spinal column is made rigid, and the head and neck are placed in a fixed position largely by the aid of the sterno-mastoid and trapezius

muscles. Such efforts cannot be made with success if the muscles in question are paralyzed. In the lower animals, according to the observations of Bernard, they also take part in the production of a cry, or prolonged vocal sound. If the entire spinal accessory be destroyed, as already shown, the voice is completely abolished by loss of power in the laryngeal muscles. If the external branch alone be divided, the animal can still produce a sound in the larynx; but this sound cannot be prolonged into a cry, and the voice is confined in duration to the ordinary length of an expiratory movement. Although the animals, furthermore, are not apparently inconvenienced by this operation so long as they remain quiet, any increased exertion, as in running or leaping, causes a want of harmony between the movements of respiration and those of the limbs, which results in unusual shortness of breath.

The sterno-mastoid and trapezius muscles, like those of the larynx, are therefore animated by two sets of motor nerve fibres. One set, coming from the cervical spinal nerves, provides for all the movements connected with ordinary changes of attitude and locomotion; the others, derived from the spinal accessory, supply the requisite stimulus for continuous muscular exertion, or for a prolonged vocal sound.

Twelfth Pair. The Hypoglossal.

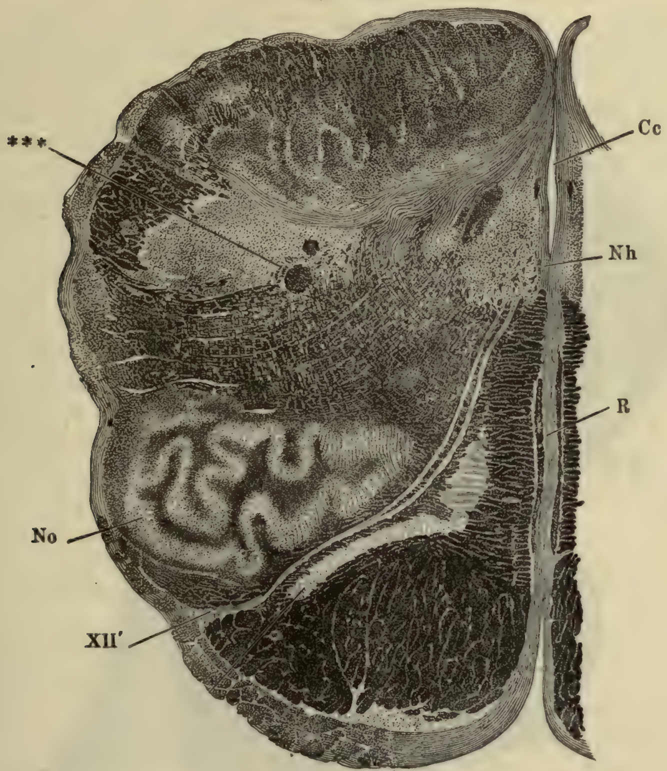
The hypoglossal nerve, the motor nerve of the tongue, emerges from the anterior part of the medulla oblongata by a linear series of ten or twelve slender filaments in the furrow between the outer edge of the anterior pyramids and the rounded projection of the olivary bodies (Fig. 179, $_5$). The vertical line along which these filaments make their appearance corresponds exactly with the line of origin of the anterior roots of the cervical spinal nerves below; and the whole external aspect of their anatomical relations resembles that of a motor nerve root.

The central origin of the hypoglossal root fibres, according to Clarke, Dean, Kölliker, Henle, and Meynert, is a nucleus of gray matter situated at the posterior part of the medulla oblongata next the median line, at the inferior extremity of the fourth ventricle. This collection of gray matter has an elongated, irregularly cylindrical form, extending longitudinally from about the level of the divergence of the posterior columns upward and forward to that of the auditory nucleus. It is, therefore, parallel in its position with the spinal accessory and pneumogastric nuclei, but situated between them and the median line. In transverse sections of the medulla, made successively from below upward, this nucleus is first seen (Fig. 180) to be placed immediately about the central canal, which is already approaching the posterior surface of the medulla; and the roots of the nerve run in a curvilinear course downward and outward to their point of emergence.

Above this point, after the central canal has opened into the cavity of the fourth ventricle (Fig. 181), the hypologlossal nucleus has itself receded quite to the posterior surface of the medulla, where it occupies

upon the floor of the fourth ventricle, on each side of the median line, the longitudinal eminence known as the "fasciculus teres." Its root fibres thence run downward through the whole thickness of the medulla

Fig. 180.



TRANSVERSE SECTION OF THE HUMAN MEDULLA OBLONGATA, just below the divergence of the posterior columns, and through the inferior extremity of the olivary nucleus.—Cc. Central canal. R. Raphe. No. Olivary nucleus. Nh. Nucleus of the hypoglossal nerve. XII'. Hypoglossal nerve roots. Magnified 8 diameters. (Henle.)

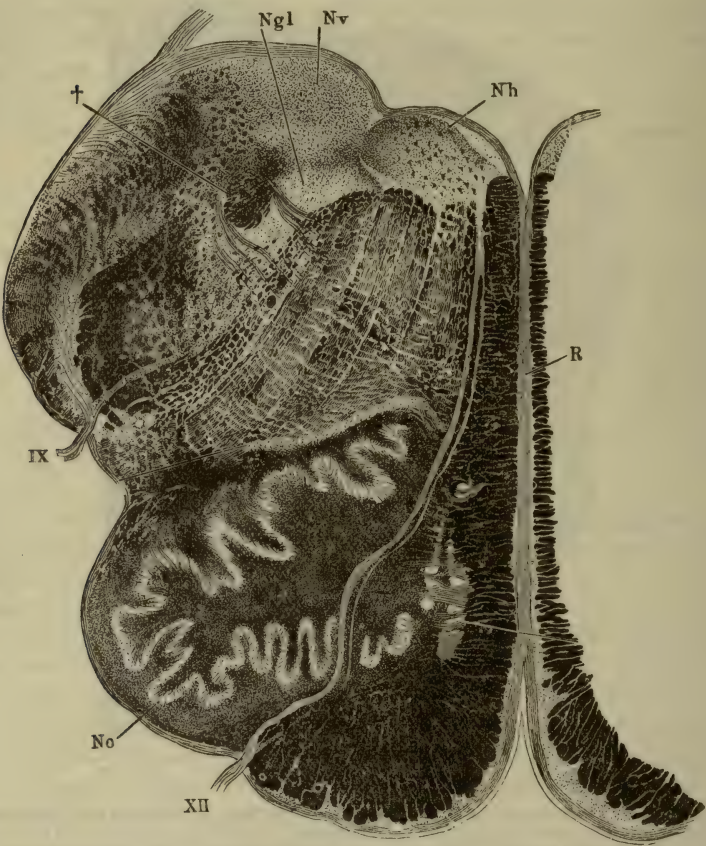
at this part, passing for some distance in a nearly vertical plane, and then curving outward, to reach the furrow between the olivary bodies and the anterior pyramids, where they emerge.

During the passage of the hypoglossal nerve roots through the medulla oblongata, they pass along the surface of the olivary nucleus, between it and the anterior pyramid, and in great measure between the folds or even through the substance of its convoluted wall. It is shown by Dean[1] that although a direct continuity cannot be made out between the root fibres of the nerve and the stellate cells of the olivary nucleus, yet prolongations of the cells can sometimes be traced for a consider-

[1] Gray Substance of the Medulla Oblongata and Trapezium. Washington, 1864, p. 36.

able distance upward and inward, in company with the nerve roots, toward the hypoglossal nucleus; and in the sheep, the tracts of fibres connecting the two nuclei are very evident. According to Henle, in some

Fig. 181.

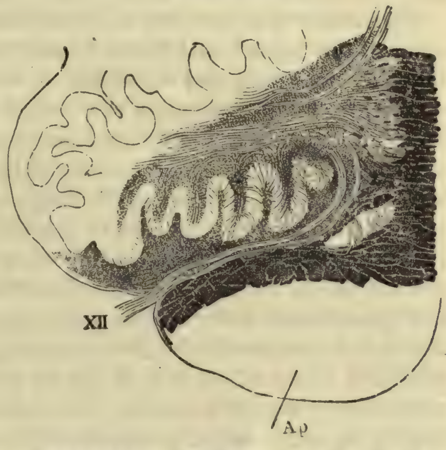


TRANSVERSE SECTION OF THE HUMAN MEDULLA OBLONGATA, through the middle of the hypoglossal nucleus and the olivary body.—No. Olivary nucleus. R. Raphe Ngl. Nucleus of the glossopharyngeal nerve. Nv. Nucleus of the pneumogastric nerve. Nh. Nucleus of the hypoglossal nerve. IX. Glossopharnygeal nerve roots. XII. Hypoglossal nerve roots. Magnified 8 diameters. (Henle.)

transverse sections through the hilum, or opening of the olivary body (Fig. 182), fibres from the hypoglossal nerve roots may be seen bending round the inner border of the nucleus into its interior; while other fibres emerge in a corresponding manner from the opposite edge of the hilum and continue onward, with the main root-bundles, to the hypoglossal nucleus. Although the details of minute anatomical structure in these parts have not been fully made out, it is evident that a close relation of some kind exists between the gray matter of the olivary bodies and the hypoglossal nucleus and roots.

Kölliker regards the roots of the hypoglossal nerves as decussating completely with each other through the raphe, at the level of the nuclei. According to both Clarke and Dean, on the other hand, a portion of the fibres of each root terminate in the corresponding nucleus, while another portion bend inward and cross the raphe at the median line, decussating with those of the opposite side. Henle describes a few thin bundles of fibres which connect the roots of the nerve on each side, at their point of emergence, with the raphe in front of the medulla. It is certain that the hypoglossal, like the other cranial nerves, has, in some way, a connection with the opposite side of the brain; since cases of facial paralysis from cerebral hemorrhage are often accompanied by paralysis of the tongue on the same side with that of the face, and on the opposite side to that of the lesion. One of the genio-hyo-glossal muscles having lost its power, while the other remains active, if the patient attempts to protrude the tongue in such cases, its point is deviated toward the paralyzed side.

Fig. 182.



TRANSVERSE SECTION OF THE HUMAN MEDULLA OBLONGATA, through the olivary nucleus and root of the hypoglossal nerve.—Ap. Anterior pyramid. XII. Hypoglossal nerve root. Magnified 8 diameters. (Henle.)

After leaving the anterior surface of the medulla oblongata the fibres of the hypoglossal nerve become parallel with each other, and, passing through the anterior condyloid foramen of the occipital bone, emerge from the skull in the form of a cylindrical cord. Immediately after escaping from the condyloid foramen it presents one or two branches of inosculation with the pneumogastric, at the point where it crosses the track of this nerve. According to Cruveilhier, the dissection of the parts, after maceration in dilute nitric acid, shows distinctly that this inosculation consists of fibres which leave the hypoglossal nerve and join those of the pneumogastric, running with them in a peripheral direction. The hypoglossal nerve then passes downward, nearly to the level of the hyoid bone, where it curves forward, giving filaments to the styloglossal and hyoglossal muscles, and to those immediately beneath the hyoid bone; after which it turns upward, penetrates the tongue from below, inosculates by two or three filaments with the lingual branch of the fifth pair, and is finally distributed to all the muscles of the substance of the tongue. It, therefore, animates not only the lingual muscles proper, but also those which draw the tongue backward and upward (styloglossal), and backward and downward (hyoglossal and infra-hyoid mus-

cles). The trunk of the nerve also receives communicating filaments from the first and second cervical spinal nerves, which, according to Cruveilhier, are filaments of reënforcement, accompanying the hypoglossal nerve toward its peripheral termination.

Physiological properties of the Hypoglossal Nerve.—The motor character of the hypoglossal nerve is easily established by the results which follow its irritation and division. If the nerve be exposed in the living or recently killed animal at the top of the neck, where it runs parallel to and a little above the hyoid bone, pinching or wounding its fibres, or the application of the galvanic stimulus, produces immediately convulsive action of the muscles of the tongue. The same effect follows if the trunk of the nerve be divided at this point, and the irritation applied to its peripheral extremity; showing that the contractions thus produced are not due to reflex action, but to a direct stimulus conveyed through the hypoglossal nerve to the muscular fibres. The excitability of the nerve is consequently beyond question. Whether it possess also any sensitive fibres of its own is not so certain. Longet obtained in this respect only negative results; the division of the filaments of origin of the nerve, in his experiments on dogs, through the space between the occiput and the atlas, not producing perceptible signs of pain. The trunk of the hypoglossal nerve outside the cranial cavity, certainly possesses some degree of sensibility, according to the testimony of nearly all experimenters; but this is regarded as derived, like that of other motor nerves, from inosculations beyond its point of origin, especially from those of the first and second cervical spinal nerves near the base of the skull, and from branches of the fifth pair near its terminal distribution. Whatever sensibility it may possess is destined only for the muscular substance of the tongue, and not for its mucous membrane; since, in the first place, division of the lingual branch of the fifth pair and of the glossopharyngeal nerve destroys both tactile and gustatory sensibility over the whole surface of the tongue, though the hypoglossal be left untouched; and secondly, according to the experiments of Longet, after division of both hypoglossal nerves in the dog the surface of the tongue, when touched with the point of a needle, evinces its ordinary tactile sensibility, the application of bitter solutions causes signs of disgust, and the contact of foreign bodies at the base of the organ excites the action of vomiting.

The distinct and uniform result of section of both hypoglossal nerves is a loss of muscular power in the whole substance of the tongue, while its tactile and gustatory sensibilities are preserved. In the experiments of Panizza, confirmed by those of Longet, the animals upon which this operation had been performed were unable to move the tongue in any direction, or even to restore it to its natural position when it was turned back, except by hanging the head downward and shaking it, thus allowing the organ to fall forward by its own weight, as a helpless mass. In the movements of the jaws, which were not interfered with, the tongue

was liable to be caught between the teeth and wounded; an accident which evidently caused suffering to the animal, thus showing the continued sensibility of the paralyzed organ.

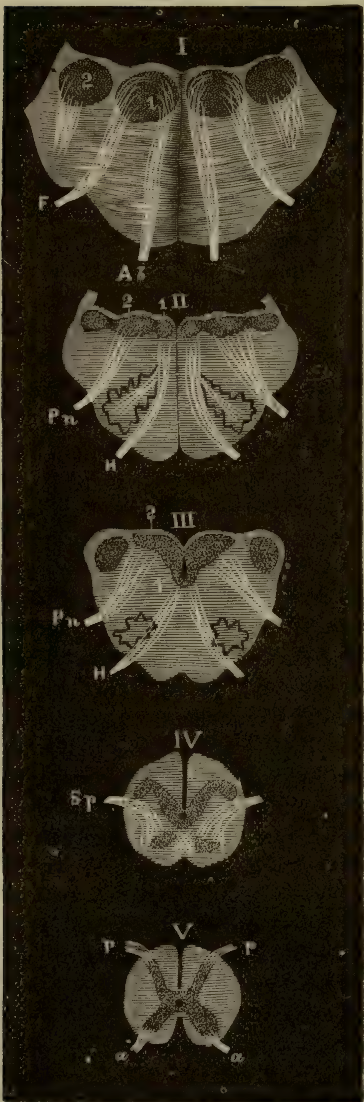
Connection of the Hypoglossal Nerve with Mastication and Deglutition.—Although the movements of the tongue do not take a direct part in mastication, they are yet of essential importance to its accomplishment, by bringing successive portions of the food between the teeth and removing those which have already undergone trituration. In species where liquids are introduced into the mouth by the act of lapping, this movement becomes also impossible after section of the hypoglossal nerves; and both liquid and solid food, the latter already reduced to a pulp, must be introduced far backward into the fauces in order to allow of their deglutition. The natural action of the lingual muscles is practically of so much importance that, according to Longet, it requires a great expenditure of time and patience, in animals with paralysis of the tongue from division of the hypoglossal nerves, to supply them with sufficient nourishment for the support of life.

Connection of the Hypoglossal Nerve with Articulation.—In man, another important function is performed by the tongue as a muscular organ, namely, that of articulation. As the lingual muscles take an important part in the pronunciation of all the consonants except the labials (*b*, *m*, *p*) and the labio-dentals (*f*, *v*), as well as in that of the vowels *a*, *e*, *i*, and *y*, their paralysis will necessarily produce a nearly complete incapacity of articulation. In man, disease or injury of the hypoglossal nerve alone is a rare occurrence, and is almost invariably confined to one side. In the glosso-labio-laryngeal paralysis, described in connection with the functions of the medulla oblongata (p. 510), the disease is of central origin, and affects, in various proportions, other muscles as well as those of the tongue. Here, however, according to Hammond, the earliest signs of imperfect action show themselves in the lingual muscles, and when the disease is fully developed the tongue becomes completely paralyzed, and all power of articulation is lost.

The hypoglossal nerve, accordingly, though one of the simplest of the cranial nerves in the nature of its physiological endowments, is essential for the expression of ideas by articulate language, and is also important as an aid in the mastication and deglutition of the food.

General Arrangement and Mode of Origin of the Cranial Nerves.—Notwithstanding the apparent irregularity in source and distribution of the cranial nerves, as compared with the spinal, an examination of their internal origin shows that they are arranged on a definite plan, not essentially dissimilar to that of the spinal nerves. The difference between them depends only upon the changed position of the gray substance in the medulla oblongata as compared with that in the spinal cord. When the central canal of the cord opens into the cavity of the fourth ventricle, just above the point of divergence of the posterior columns, the gray matter surrounding it becomes posterior instead of

Fig. 183.



I. Transverse Section of the Tuber Annulare, through the lower border of the pons Varolii. 1. Nucleus of the facial and abducens nerves. 2. Nucleus of the auditory nerve. F. Facial nerve. Ab. Abducens nerve.

II. Transverse section of the medulla oblongata, through the middle of the olivary bodies, and just above the opening of the central canal. 1. Hypoglossal nucleus. 2 Pneumogastric nucleus. H. Hypoglossal nerve. Pn. Pneumogastric nerve.

III. Transverse section of the medulla, through the lower end of the olivary bodies, and just below the opening of the central canal. 1. Hypoglossal nucleus. 2. Pneumogastric nucleus. H. Hypoglossal nerve. Pn. Pneumogastric nerve.

IV. Transverse section of the medulla, through the decussation of the anterior pyramids. Sp. Spinal accessory nerve.

V. Transverse section of the spinal cord in the dorsal region. *a*, *a*. Anterior nerve roots. *p*, *p*. Posterior nerve roots.

central in its position; what corresponds to the posterior horns of gray matter in the cord spreading out laterally, and what corresponds to the anterior horns following the central canal as it recedes, and at last occupying the middle of the floor of the fourth ventricle, next the median line. All the sensitive and motor cranial nerves take their origin from this layer of gray matter, or its continuation, from the commencement of the fourth ventricle to the aqueduct of Sylvius beneath the tubercula quadrigemina. The relations of origin between the motor and sensitive nerve roots are still preserved. In the spinal cord, the motor roots originate from the anterior horns of gray matter, the sensitive roots from the posterior horns. In the medulla oblongata and tuber annulare, the nuclei of the motor cranial nerves form a series near the median line; those of the sensitive nerves are placed farther outward. A series of sections of the spinal cord, medulla oblongata, and tuber annulare, made in succession from below upward, show that the collections of gray matter, or nuclei, in the medulla oblongata and tuber annulare, from which the different motor or sensitive nerves take their origin, are not completely disconnected from each other any more than the successive portions of gray matter in the spinal cord;

but at certain points, the gray substance takes on a special degree of development, and presents an abundant collection of nerve cells. These collections are called the "nuclei" of the nerves, on account of their evident importance as points of origin from which the nerve roots can be traced to their points of emergence at the base of the brain. The foregoing diagram shows the changes in external form of the cerebro-spinal axis, and in the position of its gray matter, as examined at different levels in the cranium and spinal canal.

CHAPTER VII.

THE SYMPATHETIC SYSTEM.

The sympathetic system of nerves, when compared with the cerebro-spinal system, presents anatomical peculiarities of arrangement and distribution so distinct and noticeable, that it is naturally regarded as occupying a place by itself. The slender double cord of its main trunk extending throughout the great cavities of the body, the number and scattered position of its ganglia, which are united with each other only by filaments of small size, the frequent and plexiform arrangement of its branches, and the distribution of its terminal fibres to the organs of circulation and nutrition, all form a well marked group of features by which it is easily recognized. But notwithstanding the general importance of these characters, the sympathetic nerves and ganglia do not constitute a separate and independent nervous system. Neither the minute structure of their anatomical elements, nor their external connections, are essentially different from those of the cerebro-spinal nerves and nervous centres. The sympathetic trunks and branches contain medullated nerve fibres of the same anatomical character as those of the spinal cord and its nerves; and its ganglia are provided with nerve cells which send off one or more prolongations in the form of nerve fibres. The main peculiarity of intimate structure in the sympathetic nerve fibres is that they are, as a rule, of small diameter, though not smaller than the average of those in the cerebro-spinal nerves. The cells of the sympathetic are also generally of comparatively small size, never, according to Kölliker, equalling the largest of those in the gray substance of the spinal cord or the brain; and they are also characterized by the frequency with which they send out only a single prolongation, thus apparently becoming a source of new fibres.

But, on the other hand, the cerebro-spinal system contains both fibres and nerve cells of small as well as large size. The posterior roots of all the spinal nerves have connected with them ganglia which are similar in structure to those of the sympathetic system; the fibres which come from the spinal cord simply passing through them, as shown by the observations of Kölliker, and being joined by other fibres originating from the gray matter of the ganglion itself. The same arrangement exists in the ganglia of the cranial nerves, as, for instance, in the Gasserian ganglion of the fifth pair. Thus all the sensitive and mixed cerebro-spinal nerves contain some fibres of ganglionic origin, in addition to those derived directly from the brain or spinal cord. Furthermore, all the sympathetic ganglia receive filaments of communi-

cation from the cerebro-spinal nerves, which, there is every reason to believe, consist of fibres coming from the brain or spinal cord, and passing through the ganglion to form part of the peripheral branches of the sympathetic system. This conclusion is drawn not only from the fact that many of these fibres cannot be shown by microscopic examination either to originate or terminate in the substance of the ganglion, but also from the paralyzing effect produced upon muscular organs supplied with sympathetic fibres, by division of the cerebro-spinal nerve which communicates with its ganglion. This is more particularly shown by the paralysis of the iris following division of the oculomotorius nerve, which gives a motor branch to the ophthalmic ganglion. The numerous branches of communication supplied by the pneumogastric nerve to the cardiac branches of the sympathetic, and to the cardiac plexus itself, afford an equally striking instance of the same kind.

The ganglia seated upon the spinal and cranial nerve roots are therefore undoubtedly analogous, in their anatomical relations, with the detached ganglia of the sympathetic system proper; and the whole of this system may be considered as made up of a set of nervous centres disseminated throughout the great cavities of the body, and of nervous filaments which both receive fibres from the cerebro-spinal centres, and communicate by some of their own with the cerebro-spinal nerves. All the organs in the body, accordingly, are supplied with fibres from both sources; the difference consisting in the proportions in which one kind or the other are present in particular parts. The cerebro-spinal nerves are supplied in the greatest abundance, and manifest their most striking properties, in the organs and functions of animal life; those of the sympathetic system preponderate in the organs of vegetative life, and in their influence upon the functions of nutrition, secretion, and growth.

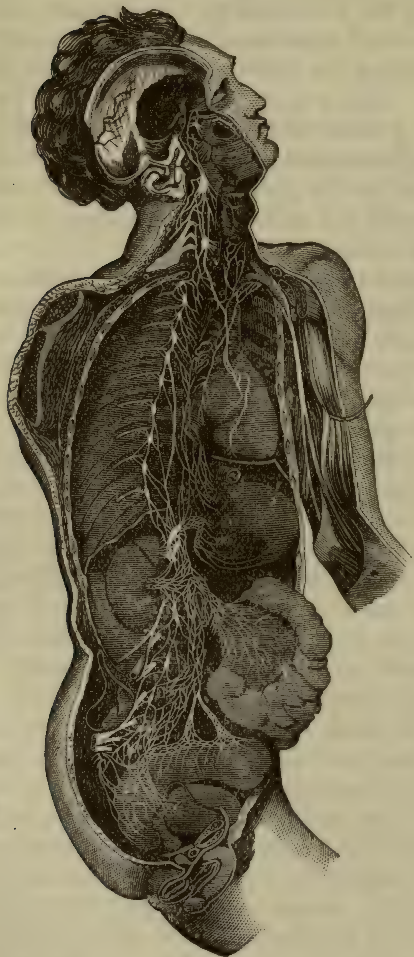
Anatomical Arrangement of the Sympathetic System.—The sympathetic system consists of a double chain of nervous ganglia, running from above downward along the front and sides of the spinal column, and connected with each other by longitudinal filaments. Each ganglion is reënforced by motor and sensitive fibres from the cerebro-spinal system, and thus the organs under its influence are brought indirectly into communication with external objects and phenomena. Its nerves are distributed to glands and mucous membranes, many of which are destitute of general sensibility, and to muscular parts which are removed from the control of the will. The sympathetic ganglia are situated successively in the head, neck, chest, and abdomen; and in each of these regions are connected with special organs by their fibres of distribution.

The first sympathetic ganglion in the head is the *ophthalmic ganglion*, situated within the orbit of the eye, on the outer aspect of the optic nerve. It communicates by slender filaments with the carotid plexus, and receives a motor root from the oculomotorius nerve, and a sensitive root from the ophthalmic branch of the fifth pair. Its filaments of distribution, known as the "ciliary nerves," pass forward upon

the eyeball, pierce the scelerotic, and terminate in the muscular tissue of the iris.

The next is the *spheno-palatine ganglion*, situated in the spheno-maxillary fossa. It communicates, like the preceding, with the carotid plexus, and receives a motor root from the facial nerve, and a sensitive root from the superior maxillary branch of the fifth pair. Its filaments are distributed to the levator palati and uvular muscles, to the mucous membrane of the posterior part of the nasal passages, and to that of the hard and soft palate.

Fig. 184.



Ganglia and Nerves of the Sympathetic System.

The third sympathetic ganglion is the *submaxillary*, situated upon the submaxillary gland. It communicates with the superior cervical ganglion of the sympathetic by filaments which accompany the facial and external carotid arteries. It derives its sensitive filaments from the lingual branch of the fifth pair, and its motor filaments from the facial nerve, by means of the chorda tympani. Its branches of distribution pass mainly to the submaxillary gland and Wharton's duct.

The last sympathetic ganglion in the head is the *otic ganglion*. It is situated beneath the base of the skull, on the inner side of the third division of the fifth pair. It receives filaments of communication from the carotid plexus; a motor root from the facial by means of the small superficial petrosal nerve, as well as one or two short fibres from the inferior maxillary division of the fifth pair; and a sensitive root from the glossopharyngeal by the nerve of Jacobson. Its branches are sent to the internal muscle of the malleus in the middle ear (tensor tympani), to the circumflexus palati, and to the mucous membrane of the tympanum and Eustachian tube.

The continuation of the sympathetic nerve in the neck consists of two and sometimes three ganglia, the superior, middle, and inferior. These ganglia communicate with each other, and also with the anterior branches of the cervical spinal nerves. Their filaments follow the course of the carotid artery and its branches, and are distributed to the substance of the thyroid gland, and to the walls of the larynx, trachea, pharynx, and œsophagus. By the superior, middle, and inferior cardiac nerves they also supply sympathetic fibres to the cardiac plexus, and, through it, to the substance of the heart.

In the chest, the sympathetic ganglia are situated on each side the spinal column, just over the heads of the ribs. Their communications with the spinal nerves in this region are double; each ganglion receiving two filaments from the intercostal nerve next above it. The filaments originating from the ganglia are distributed upon the thoracic aorta, and to the lungs and œsophagus.

In the abdomen, the continuation of the sympathetic system consists mainly of the aggregation of ganglionic enlargements situated upon the cœliac artery, known as the *semilunar* or *cœliac ganglion*. From this ganglion a multitude of radiating and inosculating branches are sent out, which, from their common origin and their diverging course, are termed the "solar plexus." From this, other plexuses originate, which accompany the abdominal aorta and its branches, and are distributed to the stomach, small and large intestine, spleen, pancreas, liver, kidneys, supra-renal capsules, and internal organs of generation.

Beside the above ganglia there are in the abdomen four other pairs, situated in front of the lumbar vertebræ. Their filaments join the plexuses radiating from the semilunar ganglion.

In the pelvis, the sympathetic system is continued by four or five pairs of ganglia, situated on the anterior aspect of the sacrum, and terminating, at the lower extremity of the spinal column, in the "ganglion impar," which is probably to be regarded as a fusion of two separate ganglia.

The entire sympathetic series is thus composed of numerous small ganglia connected throughout, first with each other; secondly, with the cerebro-spinal system; and thirdly, with the viscera.

Physiological Properties of the Sympathetic Ganglia and Nerves.—The properties and functions of the sympathetic nerves have been less successfully studied than those of the cerebro-spinal system, owing, perhaps, to the anatomical difficulties in the way of reaching and operating upon them for purposes of experiment. The principal part of the sympathetic system is situated in the interior of the chest and abdomen; and the mere opening of these cavities, to reach the ganglionic centres, causes such a disturbance in the functions of vital organs, and such a shock to the system at large, that the results of these experiments are liable to be more or less unsatisfactory. The connections of the sympathetic ganglia with each other and with the cerebro-spinal axis are so numerous and scattered, that these ganglia cannot be completely isolated without resorting to a still more extensive operation. And finally, the

sensible phenomena obtained by experimenting on the sympathetic nerves are, in many cases, slow in making their appearance, and not particularly striking or characteristic in their nature.

Notwithstanding these difficulties, however, some facts have been ascertained with regard to this part of the nervous system, which give a certain degree of insight into its character and functions.

Influence on Movement and Sensibility.—The sympathetic system is endowed both with sensibility and the power of exciting motion ; but these properties are less active than in the cerebro-spinal system, and are exercised in a different manner. If we irritate a sensitive spinal nerve in one of the limbs, or apply the galvanic current to its posterior root, the evidences of pain or of reflex action are decisive and instantaneous. There is no appreciable interval between the application of the stimulus and the sensation which results from it. On the other hand, in experiments upon the sympathetic ganglia and nerves, evidences of sensibility are also manifested, but much less acutely, and only after somewhat prolonged application of the irritating cause. These results correspond with what we know of the physiological properties of the organs supplied by the sympathetic system. These organs are insensible, or nearly so, to ordinary impressions. We are not conscious of the changes going on in them, so long as they retain a normal character. But they are still capable of perceiving unusual or excessive irritations, and may even give rise to acute pain when in a state of inflammatory alteration.

There is the same peculiar character in the action of the motor nerves belonging to the sympathetic system. If the facial or hypoglossal, or the anterior root of a spinal nerve, be irritated, the convulsive movement which follows is instantaneous, spasmodic, and momentary in duration. But if the semilunar ganglion or its nerves be subjected to a similar experiment, no immediate effect is produced. It is only after a few seconds that a slow, vermicular, progressive contraction takes place in the corresponding part of the intestine, which continues for some time after the exciting cause has been removed.

Morbid changes taking place in organs supplied by the sympathetic present a similar peculiarity in their production. If the body be exposed to cold and dampness, congestion of the kidneys shows itself perhaps on the following day. Inflammation of any internal organ is rarely established within twelve or twenty-four hours after the application of the exciting cause. The internal processes of nutrition, together with their derangements, which are more especially under the control of the sympathetic, require a longer time to be influenced by incidental causes, than those which are regulated by the cerebro-spinal system.

Connection with the Special Senses.—In the head, the sympathetic has an important connection with the special senses. This is noticeable more particularly in the case of the eye, in the influences regulating the expansion and contraction of the pupil. The ophthalmic ganglion sends off a number of ciliary nerves, distributed to the iris, and receives a

motor root from the oculomotorius. The reflex action, by which the pupil contracts under the influence of light and expands under its diminution, takes place, accordingly, through this ganglion. The impression conveyed by the optic nerve to the tubercula quadrigemina, and reflected outward by the fibres of the oculomotorius, is not transmitted directly by the last named nerve to the iris; but passes first to the ophthalmic ganglion, and is thence conveyed to its destination by the ciliary nerves.

The reflex movements of the iris exhibit consequently a somewhat sluggish character, which indicates the intervention of the sympathetic system. The changes in the size of the pupil do not take place instantaneously with the variation in the amount of light, but require an appreciable interval of time. If we suddenly pass from a light into a dark room, we are unable to distinguish surrounding objects until a certain time has elapsed, and the expansion of the pupil has taken place; and vision even continues to grow more distinct for a considerable period afterward, as the expansion of the pupil becomes more complete. If we cover the eyes of another person with the hand or a folded cloth, and then suddenly expose them to the light, we can see that the pupil, which is at first dilated, contracts somewhat rapidly to a certain extent, and afterward continues to diminish in size for several seconds, until its equilibrium is fairly established. Furthermore, if we pass suddenly from a dark room into bright sunshine, we are immediately conscious of a painful impression in the eye, which results from the inability of the pupil to contract with sufficient rapidity. All such exposures should therefore be made gradually, in order that the movements of the iris may keep pace with the varying quantity of stimulus, and thus protect the eye from injurious impressions.

The reflex movements of the iris, though accomplished through the medium of the ophthalmic ganglion, derive their original stimulus, through the motor root of this ganglion, from the oculomotorius nerve. For if the oculomotorius nerve be divided between the brain and the eyeball, the pupil becomes sensibly dilated, and loses in great measure its power of contracting under the influence of light. The motive power, originally derived from the brain, is, therefore, modified by passing through the ophthalmic ganglion before reaching its destination in the iris.

Three organs of special sense, the eye, the nose, and the ear, are each provided with two sets of muscles, superficial and deep, which regulate the quantity of stimulus admitted to the organ and the mode in which it is received. The superficial set is animated by branches of the facial nerve; the deep-seated or internal set, by filaments from a sympathetic ganglion.

Thus, the front of the eyeball is protected by the orbicularis and levator palpebræ superioris muscles, which open or close the eyelids at will, and allow a larger or smaller quantity of light to reach the cornea. These muscles are supplied by the oculomotorius and facial nerves, and

are mainly voluntary in their action. The iris, on the other hand, is a deep-seated muscular curtain, which regulates the quantity of light admitted through the pupil. It is supplied by filaments from the ophthalmic ganglion, and its movements are involuntary.

Division of the sympathetic nerve in the middle of the neck has a marked effect on the muscular apparatus of the eye. Within a few seconds after this operation has been performed upon the cat, the pupil of the corresponding eye becomes contracted, and remains in that condition. At the same time the third eyelid, or "nictitating membrane," with which these animals are provided, is drawn partially over the cornea, and the upper and lower eyelids also approximate to each other; so that all the apertures guarding the eyeball are perceptibly narrowed, and the expression of the face on that side is altered in a corresponding degree. This effect has been explained by supposing the circular fibres of the iris, or the constrictors, to be animated by filaments derived from the oculomotorius, and the radiating fibres, or the dilators, to be supplied by the sympathetic; so that, while division of the oculomotorius would produce dilatation of the pupil by paralysis of the circular fibres only, division of the sympathetic would be followed by exclusive paralysis of the dilators, and consequently by contraction of the pupil. This explanation, however, is not entirely satisfactory; since, after division of the sympathetic nerve in the cat, not only is the pupil contracted, but both the upper and lower eyelids and the nictitating membrane are also drawn partially over the cornea, and assist in excluding the light. The last-named effect cannot be owing to direct paralysis, from division of the fibres of the sympathetic. It is more probable that the section of this nerve operates by exaggerating for a time the sensibility of the retina, owing to vascular congestion; and that the partial closure of the eyelids and pupil is a consequence of that condition.

Fig. 185.

CAT, after section of the right sympathetic.

In the olfactory apparatus, the superficial set of muscles are the compressors and elevators of the alæ nasi, which are animated by filaments of the facial nerve. By their action, odoriferous vapors are snuffed up and directed into the upper part of the nasal passages, where they come in contact with the sensitive portions of the olfactory membrane; or, if too pungent or disagreeable in flavor, are excluded from entrance. These muscles are not very important in the human species; but in many of the lower animals, as in the carnivora, they play a very important part in the mechanism of olfaction. Furthermore, the levators and depressors of the velum palati, which are deep-seated, serve to open

or close the posterior nares, and accomplish a similar office with the muscles already named in front. The levator palati and uvular muscles are supplied by filaments from the spheno-palatine ganglion, and are involuntary in character.

The ear has two sets of muscles, similarly supplied. The superficial set are those attached to the external ear. They are comparatively inactive in man, but in many of the lower animals are well developed and important. In the horse, the deer, the sheep, and various other species, they turn the ear in different directions to catch more distinctly feeble sounds, or to exclude those which are disagreeable. These muscles are supplied by filaments of the facial nerve, and are voluntary in their action.

The deep-seated set are the muscles of the middle ear. Sounds are transmitted to the middle ear through the membrane of the tympanum, which may be made more or less sensitive to sonorous impressions by varying its condition of tension or relaxation. This condition is regulated by the two muscles of the middle ear, namely, the tensor tympani and the stapedius. The first named muscle is supplied with nervous filaments from the otic ganglion of the sympathetic. By its contraction, the handle of the malleus is drawn inward, bringing the membrana tympani with it, and thus increasing its tension. On the relaxation of the muscle, the chain of bones returns to its ordinary position, and the previous condition of the tympanic membrane is restored. This action, so far as we can judge, is purely involuntary. The stapedius muscle, on the other hand, is supplied by a branch of the facial nerve (p. 549). It is probable that its contraction serves to relax the membrana tympani, and enables us to make a certain degree of voluntary exertion in listening for faint or distant sounds.

Connection with the Circulation.—Perhaps the most important fact concerning the sympathetic system is that of its influence over the vascularity of the parts supplied by it. In the first place, division of the sympathetic trunk produces a *vascular congestion in the corresponding parts.* If this nerve be divided, in any of the warm-blooded quadrupeds, in the middle of the neck, a vascular congestion of all parts of the head, on the corresponding side, immediately follows. This congestion is most distinctly evident in the rabbit, in the thin and transparent ears; and within a few minutes after the operation, the difference in their appearance on the two sides is strongly pronounced. All the vessels of the ear on the affected side become turgid with blood; and many which were before imperceptible, are distinctly apparent. This effect, which was first pointed out by Bernard, and has been observed by many other experimenters, we have often verified. It lasts for a considerable time, and may even be very distinct at the end of three weeks. It remains longer when a portion of the nerve has been cut out, or the cervical ganglion extirpated, than when its filaments have been simply divided by a transverse section. It finally disappears when the separated filaments have reunited and regained their functional activity.

The vascular congestion thus produced by division of the sympathetic nerve is accompanied by three important phenomena, all intimately connected with each other.

First, the quantity of blood circulating in the part is increased, and its movement accelerated. It is not a state of passive congestion; but all the vessels are simultaneously dilated, a larger quantity of blood passes through the capillaries in a given time, and returns by the veins in greater abundance than before.

Secondly, there is a remarkable elevation of temperature in the affected part. This elevation of temperature is very perceptible to the touch, both in the ear and in the integument of the corresponding side of the head. Measured by the thermometer, it has been found by Bernard to reach, in some cases, 4.5 or 5 degrees (8° or 9° F.). It results from the increased quantity of blood circulating in the vessels; since the blood coming from the interior and warmer parts of the body supplies more heat, in proportion to the abundance and rapidity with which it traverses the vascular tissues.

Thirdly, the color of the venous blood becomes brighter. This effect is also due to increased rapidity of the circulation. The blood is deprived of its oxygen and darkened in color by the changes of nutrition which take place in the tissues. But if the rapidity of the circulation be suddenly increased, a certain proportion of the blood escapes deoxidation, and its change in color, from arterial to venous, is incomplete. The blood accordingly returns by the veins of the affected part in greater abundance, of a higher temperature, and of a more ruddy color, than in the corresponding parts on the opposite side.

When a local vascular congestion has thus been produced by division of the sympathetic nerve, if that portion of the divided nerve which remains in connection with the tissues be galvanized, all the above effects rapidly disappear; the bloodvessels of the ear and corresponding side of the head contract to their previous dimensions, the quantity of blood circulating through the tissues is diminished, the temperature is reduced in a corresponding degree, and the blood in the veins returns to its ordinary dark color. The variations in the rapidity of the circulation, dependent on the condition of the sympathetic nerve, have been shown by Bernard[1] in the following manner. In a living rabbit the upper part of one ear is cut off with a pair of very sharp scissors, so that the blood may escape in jets from the divided ends of the small arteries. The force and height of the arterial jets having been observed, the sympathetic nerve is then divided in the middle of the neck on the corresponding side. Immediately the blood escapes from the wounded ear in greater abundance, and the arterial jets rise to double or even triple their former height. The galvanic current is then applied to the divided extremity of the sympathetic, above the point of section, when the streams of blood escaping from the wound diminish or disappear; but

[1] Journal de la Physiologie de l'Homme et des Animaux. Paris, 1862, p. 397.

they recommence and again increase in intensity so soon as the galvanization of the nerve is suspended.

The same author has shown that a similar influence is exerted by the sympathetic nerve upon the circulation in the limbs.[1] If the lumbar nerves of one side be divided, in the dog, within the cavity of the spinal canal, paralysis of motion and sensibility is produced in the corresponding limb, but there is no change in its vascularity or temperature; while if the lumbar portion of the sympathetic be divided or excised, without disturbing the spinal nerves, all the signs of increased temperature and activity of the circulation are manifested in the limb below, without loss of motion or sensibility. Exsection of the first thoracic ganglion of the sympathetic produces similar effects in the anterior extremity; and these effects are diminished or suspended by electric irritation of the divided nerve.

Division of the sympathetic nerve, accordingly, produces dilatation of the bloodvessels and consequent increased rapidity of the circulation, and causes the blood to retain its red color in the veins; while galvanization of the same nerve produces contraction of the vessels, diminishes the quantity of the circulating fluid, and causes the change in color of the blood, from arterial to venous.

The same thing takes place in the glandular organs. If the submaxillary or parotid gland be exposed in the living animal,[2] so long as the gland is in its ordinary condition the blood passing through it is seen to undergo the usual changes, and returns dark colored by the veins. But if the sympathetic filament which accompanies the external carotid artery be divided, the quantity of blood flowing through the gland is at once increased, and appears of a red color in the veins. The same changes occur when the gland is excited to secretion by stimulating the organs of taste.

An apparent antagonism exists, in regard to the circulation, between the sympathetic nerve and those derived from the cerebro-spinal system. If the chorda tympani, which sends filaments to the submaxillary ganglion, be galvanized, it causes an excitement of the secretion[3] in the submaxillary gland, increased activity of the circulation, and a red color of the blood in the veins. The division of this nerve is followed by a contrary result. The effects produced, therefore, by galvanization of the chorda tympani are those produced by division of the sympathetic; and the effects produced by galvanizing the sympathetic are those which follow division of the chorda tympani.

The vascularity of the parts, accordingly, as well as the glandular activity of vascular organs, are under the control of the nervous system. The filaments of the sympathetic nerve accompany everywhere the bloodvessels, enveloping the arterial branches with an abundant plexus, and

[1] Journal de la Physiologie de l'Homme et des Animaux. Paris, 1862, p. 397.

[2] Bernard, Leçons sur les Liquides de l'Organisme. Paris, 1859, tome i. p. 230.

[3] Leçons sur les Liquides de l'Organisme. Paris, 1859, tome i. p. 312.

following them to their minutest ramifications. They appear to act by causing a contraction in the organic muscular fibres of the small arteries, thus regulating the resistance of the vessels, and the passage of the blood through them. When the sympathetic nerve is excited, the vessels contract, the blood passes through them slowly, and is fully converted, during its passage, into venous blood. When the influence of this nerve is diminished or suspended, the vessels dilate, and the blood, passing through them with greater rapidity, is not completely changed from the arterial to the venous condition.

Connection with Reflex Actions.—The influence of the sympathetic nerve upon the thoracic and abdominal viscera has been only imperfectly investigated. It undoubtedly serves as a medium of reflex action between the sensitive and motor portions of the digestive, excretory, and generative apparatus; and it is certain that it takes part in reflex actions in which the cerebro-spinal system is also interested. There are accordingly three different kinds of reflex action, taking place wholly or partially through the sympathetic system, which may occur in the living body.

1. *Reflex actions taking place from the internal organs, through the sympathetic and cerebro-spinal systems, to the voluntary muscles and sensitive surfaces.*—The convulsions of children are often due to the irritation of undigested food in the intestinal canal. Attacks of indigestion may also produce temporary amaurosis, double vision, strabismus, and even hemiplegia. Nausea, and a diminished or capricious appetite, are prominent symptoms of early pregnancy, induced by the condition of the uterine mucous membrane.

2. *Reflex actions taking place from the sensitive surfaces, through the cerebro-spinal and sympathetic systems, to the involuntary muscles and secreting organs.*—Exposure of the integument to cold and wet is often a determining cause of diarrhœa. Mental and moral impressions, excited through the special senses, will affect the motions of the heart, and disturb the acts of digestion and secretion. Terror, or an absorbing interest of any kind, will produce dilatation of the pupil, and communicate in this way an unusual expression to the eye. Disagreeable sights or odors, or even unpleasant occurrences, are capable of hastening or arresting the menstrual discharge, or of inducing premature delivery.

3. *Reflex actions taking place, through the sympathetic system, from one part of the internal organs to another.*—The contact of food with the mucous membrane of the intestine excites a peristaltic movement in its muscular coat. The mutual influence of the digestive, urinary, and internal generative organs upon each other is exerted through the medium of the sympathetic ganglia and nerves. The variations of the capillary circulation in different abdominal viscera, corresponding with the activity or repose of their associated organs, are due to a similar nervous influence. These phenomena are not accompanied by conscious sensation, nor by any apparent intervention of the cerebro-spinal system.

CHAPTER VIII.

THE SENSES.

THE senses are the endowments by which we perceive the physical properties of external objects and the phenomena produced by their various reactions, such as solidity, pressure, smoothness or inequality of surface, temperature, light, sound, and sapid and odoriferous qualities. All our information with regard to the objects of nature is obtained through these channels, which are consequently the primitive source of all conscious relation with the external world. Sensation alone indicates merely the perception of some impression derived from without, whatever may be its nature. The senses, on the other hand, form so many subdivisions of the main function, each of which is devoted to the perception of a particular class of physical properties or reactions. They are divided into five different groups, namely: 1. General sensibility. 2. The sense of taste. 3. The sense of smell. 4. The sense of sight. 5. The sense of hearing.

General Sensibility.

General sensibility is that by which we appreciate the simpler physical properties of external objects, such as their consistency, roughness or smoothness of surface, temperature, and mass. It is so called because it is generally diffused over the external integument, beside being present in most of the mucous membranes near the surface. Notwithstanding that this endowment includes the power of perceiving several different kinds of impression, they are all, so far as we know, communicated to the perceptive centres by the same nerves; and the grade of sensibility for all varies, as a general rule, in the same direction and to the same degree in different parts of the body. The sensations thus produced, though presenting some peculiarities by which they may be distinguished from each other, are therefore naturally comprised under the single head of general sensibility.

Sensations of Touch.—This is, perhaps, the least complicated form of sensory impression, and is known as "tactile sensibility." It is produced by the simple contact of a foreign body with the sensitive surface, and gives information as to its solidity, its external configuration, and its indifferent or irritating qualities. Although there is a certain variety in these impressions, yet they evidently belong to the same group, and there is no essential difference in the effect produced by the contact of sharp-pointed instruments, and that caused by irritating substances, like mustard, applied to the skin, the continuous or

interrupted galvanic current, pungent liquids placed upon the tongue, or pungent vapors in the nasal passages. These are all impressions of tactile sensibility, and depend upon a similar irritation of the peripheral nervous extremities.

The structures especially devoted to the exercise of tactile sensibility are minute bulbous organs developed upon the terminal extremities of the nerve fibres in the papillæ of the skin and adjacent mucous membranes, in each of which two situations they present certain distinguishing features, though their essential character is the same in both. In the skin, these organs are known as the *tactile corpuscles.* They are elongated oval bodies, measuring, according to Kölliker, about $\frac{1}{10}$ of a millimetre in length by $\frac{1}{20}$ of a millimetre in thickness. They are situated in the substance of certain of the papillæ, with their long axes placed longitudinally, and extending nearly to the free extremity of the organ. They are not to be found in all of the papillæ, since even at the end of the index finger, where they are most abundant, according to the observations of Meissner, not more than one papilla in four is provided with a tactile corpuscle. The papillæ containing the corpuscles are not supplied with bloodvessels; while the remainder, constituting the large majority, contain capillary bloodvessels, but no tactile corpuscles. The tactile corpuscle itself consists, 1st, of a sheath, exhibiting a number of transverse nuclei, and considered as representing a form of connective tissue; 2d, of an inclosed mass of transparent, homogeneous material; and, 3d, of one or two medullated nerve fibres, which pass upward from the superficial plexus of the skin through the substance of the papilla, reach the tactile corpuscle, wind round it in a spiral direction toward its apex, and finally, losing their medullary layer, terminate in some manner not yet distinctly ascertained. Tactile corpuscles have been found, in man, upon the dorsal and palmar surfaces of the hand and foot, upon the nipple, and upon the anterior part of the forearm. As their abundance in these different regions corresponds with the local acuteness of sensibity, they are undoubtedly to be regarded as the special organs of touch, though not perhaps the only form of nerve structure capable of exercising this function.

Fig. 186.

Papilla of the Human Skin, containing tactile corpuscle and nerve fibres. (Kölliker.)

In the conjunctiva, the red portion of the lips, the tongue, the sublingual mucous membrane, and the glans penis, the organs of touch are constituted by the *terminal bulbs* of the nerve fibres in these regions. These organs differ from the tactile corpuscles mainly in their smaller size and the greater simplicity of their structure. In man, according to Kölliker, they are for the most part nearly spherical in form, though in the inferior animals they are often elongated and club-shaped. They

consist of a very thin, external envelope of connective tissue, inclosing, as in the tactile corpuscle, a mass of homogeneous or finely granular substance. The medullated nerve fibre which penetrates the bulb, loses its medullary layer at its entrance, and runs through the central homogeneous substance, to terminate by a free extremity near its apex. Both the tactile corpuscles and the terminal bulbs are therefore anatomical forms, in which the axis cylinder of the sensitive nerve fibre terminates, after divesting itself of its medullary layer.

The tactile sensibility varies considerably in different regions of the integument. The best method of appreciating this variation is that adopted by Weber and Valentin. It consists in applying to different parts the points of a pair of compasses, tipped with suitable pieces of cork. If these points be applied to the skin when fixed at very short distances apart, the two sensations cannot be accurately distinguished from each other but are blended into one; and the impression thus produced is that of a single contact. The minimum distance at which the two points can be distinguished by the integument thus becomes a measure of its sensibility at that spot. The observations of Valentin,[1] which are the most varied and complete in this respect, give the following as the limits of distinct perception in different regions:

Distance at which two points may be separately distinguished.

At the tip of tongue	1.00	millimetre.
" palmar surface of tips of fingers	1.50	"
" " " of second phalanges	3.24	"
" " " of first phalanges	3.44	"
" dorsum of tongue	5.22	"
" dorsal surface of fingers	8.12	"
" cheek	9.46	"
" back of hand	14.50	"
" skin of throat	17.27	"
" dorsum of foot	26.10	"
" front of sternum	33.07	"
" middle of back	50.43	"

This method does not necessarily give an absolute measure of the *acuteness* of sensibility in the different regions, since the two points might be less easily distinguished from each other in any one region, and yet the absolute amount of sensation produced might be as great as in the surrounding parts; but it undoubtedly affords an accurate estimate of the *delicacy* of tactile sensation, by which we distinguish slight inequalities in the surface of solid bodies. There is every reason to believe that the two qualities of delicacy and acuteness of local sensibility correspond with each other in their degree of development in various localities; since the regions where tactile sensibility is most delicate are frequently found to be also those where the amount of sensation is the greatest. A feeble galvanic current may be perceived

[1] In Todd's Cyclopædia of Anatomy and Physiology, vol. iv., article on Touch.

when applied to the tips of the fingers, though it will produce no impression on the rest of the limbs or trunk; and one which is too faint to be distinguished by the fingers may be perceptible at the tip of the tongue.

Certain parts of the body, furthermore, are especially well adapted for use as organs of touch, not only on account of their acute sensibility, but also owing to their conformation and mobility. In man, the hands are the most favorably constructed for this purpose, by the numerous articulations and varied power of movement of the fingers, by which they may be applied to solid surfaces of any form, and brought successively in contact with all their irregularities and depressions. We are thus enabled to obtain the most precise information as to the texture, consistency, and configuration of foreign bodies.

But the hands are not the exclusive organs of touch, even in man, and in the lower animals the function is mainly performed by other parts. In the cat and in the seal, the long bristles seated upon the lips are used for this purpose, each bristle being connected at its base with a nervous papilla; and in the elephant the end of the nose, which is developed into a flexible and sensitive proboscis, is employed as the principal organ of touch. This function, therefore, may be performed by one part of the body or another, provided the accessory organs be developed in a favorable manner.

About the head and face, the sensibility of the skin is principally dependent upon branches of the fifth pair. In the neck, trunk, and extremities it is due to the sensitive fibres of the cervical, dorsal, and lumbar spinal nerves. It exists, to a considerable extent, in the mucous membranes of the mouth and nose, and of other passages leading to the interior. The sensibility of the mucous membranes is most acute in parts supplied by branches of the fifth pair, namely, the conjunctiva, anterior part of the nares, inside of the lips and cheeks, and the anterior two-thirds of the tongue. The tactile sensibility, which is resident in the skin and in a certain portion of the mucous membranes, diminishes in degree from without inward, and disappears altogether in the internal organs which are not abundantly supplied with nerves from the cerebro-spinal system.

While the general sensibility of the skin, and of the mucous membranes, varies in acuteness in different parts of the body, it is *everywhere the same in kind.* The tactile sensations produced by the contact of a foreign body are of the same nature, whether they be felt by the tips of the fingers, the dorsal or palmar surfaces of the hands, the lips, cheeks, or any other part of the integument. Their only difference is in the intensity and distinctness of the impressions produced.

The appreciation of the *weight* or mass of a foreign body is obtained from the degree of pressure which it causes upon the integument, when supported by the hand or other part of the body. It does not appear that any other kind of sensation is necessary for this purpose, although we generally also employ, in estimating a weight, the degree of muscular effort required to sustain it. If the hand, however, be rested upon some

solid support, and the foreign body placed upon it, its weight is then appreciated solely by the amount of pressure which it causes. The sensation of muscular contraction is itself a result, so far as we can judge, of the physical impression produced upon the sensitive nerve fibres in the muscular tissue; and there is nothing to indicate that it differs essentially from that caused by pressure upon the nerves of the integument.

Sensations of Temperature.—The appreciation of temperature is also most highly developed, as a general rule, in those parts which have the greatest share of tactile sensibility. The difference in this respect between the integument of the face and that of the scalp is very marked; since hot applications may be readily borne upon the scalp, which would be nearly or quite intolerable upon the face. The extent of surface exposed to a given temperature has also an influence upon the effect produced, and a moderate degree of either warmth or cold applied over a considerable portion of the skin is much more readily perceived than if confined to a limited region. There is evidence that the impressions of temperature and those of touch, if transmitted by the same fibres, depend upon two different forms of nervous excitation, or are received by different peripheral nervous structures; since abundant instances have been observed in which one of these two kinds of sensibility was impaired independently of the other. In various forms of paralysis, tactile sensibility may be lost while that of temperature remains; or, on the other hand, the power of appreciating temperatures may disappear while impressions of contact continue to be perceived.[1]

Sensations of Pain.—The sense of pain is different in character from that caused by tactile impressions or by variations in temperature. It is caused by any exaggerated mechanical irritation or by the application of excessive heat or cold; but in all these instances, when the intensity of the impression rises above a certain point, the ordinary perceptions produced by it disappear, and that of pain takes their place. Thus if the blade of a knife or the point of a needle be placed gently in contact with the skin, we perceive, by means of tactile sensibility, the character and form of its surface. But if the pressure be increased beyond a certain degree, or if the integument be actually wounded, we obtain no precise information of the physical qualities of the foreign body, and are only conscious of the pain which results. The appreciation of cold or warmth, in like manner, is only possible within moderate limits; and when the variations are so excessive as to produce pain, all accurate perception of the degree of temperature is lost. The contact of a red-hot iron and that of one much below the freezing point of water produce sensations which are not essentially different from each other, and which are marked only by their painful character.

It is not known whether the sensation of pain be confined to nerve

[1] Brown-Séquard, Physiology and Pathology of the Central Nervous System. Philadelphia, 1860, pp. 84, 98, 125.

fibres which are distinct from those endowed with other forms of general sensibility, but it is certain that it may be preserved or lost independently of the other varieties. The anæsthesia which is produced by the inhalation of ether or chloroform may be carried to such a point that the capacity for feeling pain is abolished, while tactile sensibility remains; so that the wounds caused by puncturing or cutting instruments may be felt, though unaccompanied by any sense of suffering. Similar observations have been made in cases of paralysis where, it is well known, the patient may perceive the contact of foreign bodies or the prick of a pin, but at the same time may not experience from them any painful sensation; or, on the other hand, the sense of pain may persist in the affected parts, while that of touch is diminished or lost.[1] Notwithstanding this apparent independence of the immediate conditions necessary for the sensation of pain, it is transmitted by fibres of the same nerves, belonging to the cerebro-spinal system, which convey ordinary impressions; and nerves which are endowed with the most acute tactile sensibility, like the branches of the fifth pair, are also capable, when irritated by injury or disease, of giving rise to the severest painful impressions.

Mode of Action of the Senses in general.—There are certain facts connected with the exercise of general sensibility which are also common to the operation of all the senses, and which are of sufficient importance to be considered by themselves.

In the first place, an impression of any kind, made upon a sensitive organ, *remains for a short time after the removal of its immediate cause.* The state of excitement produced in the nervous expansions and fibres has a certain degree of persistence, which is longer in duration for some organs than for others, but which exists in some degree for all. The sense of simple contact or pressure of a foreign body upon the skin, especially if it be somewhat forcible and continued, remains for a perceptible interval after the foreign body is removed. The feeling of cold or warmth, from the application of ice or heated liquids, lasts more or less after the application is discontinued. Even in the case of sight and hearing it is easy to verify the same fact; and the duration of continuance of the nervous impression, though very short, has been found in many instances susceptible of measurement.

Secondly, the organs of sense after a time *become accustomed to a continued impression*, so that they no longer perceive its existence. If a uniform pressure be exerted upon any part of the body, the compressing substance at last fails to excite sensation, and we remain unconscious of its existence. In order to attract our notice, it is necessary to increase or diminish the pressure or to change its locality or direction.

The olfactory apparatus also becomes habituated to odors, whether agreeable or disagreeable in their nature, in the confined air of a close

[1] Brown-Séquard, Physiology and Pathology of the Central Nervous System. Philadelphia, 1860, pp. 97, 126. Hammond, Diseases of the Nervous System. New York, 1871, p. 82.

apartment; although, on first entering from without, the attention may have been attracted by them in a decided manner. A continuous and uniform sound, like the steady rumbling of carriages, or the monotonous hissing of boiling water, becomes after a time inaudible; but as soon as the sound ceases, we notice the alteration, and our attention is at once excited. The senses, accordingly, receive their stimulus more from the variation and contrast of external impressions, than from these impressions themselves.

Another important particular, in regard to the senses, is their *capacity for education.* The touch can be so trained that the blind may read words and sentences by its aid, in raised letters, where an ordinary observer would hardly detect more than a slight inequality of surface. The educated eye of the artist or the naturalist will distinguish variations of color, size, and outline, quite inappreciable to ordinary vision; and the senses of taste and smell, in those who are in the habit of examining wines and perfumes, acquire a similar superiority of discriminating power.

In these instances, it is not the organ of sense itself which becomes more perfect in organization, or more susceptible to sensitive impressions. The functional power, developed by cultivation, depends upon the increased delicacy of the *perceptive* and *discriminating* faculties. It is a mental and not a physical superiority which gives the painter or the naturalist a greater facility for distinguishing colors and outlines, and which enables the medical observer to detect nice variations in the sounds of the heart or the respiratory murmur of the lungs. The impressions of external objects, to produce their complete effect, must first be received by a sensitive apparatus, which is perfect in organization and functional activity; and, secondly, they must be subjected to the action of an intelligent perception, by which their nature, source, and relations are fully appreciated.

Beside the endowment of general sensibility distributed over the integument, there are other faculties by which we appreciate particular physical qualities or phenomena, namely, those of taste, odor, light, and sound, the exercise of which is confined to special organs, having a structure adapted to that purpose alone. These are called the *special senses.* Their organs differ from the general integument in their more complicated structure and in the delicate and varied character of the functions which they perform. They are incapable of feeling pain, similar to that perceived by the nerves of general sensibility, though they may communicate disagreeable as well as pleasing impressions. The light, however intense, has no perceptible effect when allowed to fall upon the skin, and causes a sensation only when admitted to the eye. The impression of sound is appreciated only by the ear, and that of odors only by the olfactory membrane. These different sensations, therefore, are not merely exaggerations of ordinary sensibility, but are peculiar in their nature, and are in relation with distinct properties of external objects.

Each organ of special sense consists—First, of a nerve, endowed with the special sensibility required for its peculiar function; and, Secondly, of certain accessory parts, forming an apparatus adapted to aid in the performance of this function, and render it more delicate and complete.

Sense of Taste.

The sense of taste is, in some measure, intermediate in character between the functions of general and special sensibility. First, the organ by which it is exercised forms a part of the mucous membrane lining the commencement of the alimentary canal, furnished with vascular and nervous papillæ analogous in structure to those of the general integument. Secondly, this mucous membrane is also endowed with general sensibility. Although it is highly probable that certain minute formations in its epithelial layer, known as "taste buds," may be especially connected with the perception of savors, there is thus far no certainty in this respect; and in any case the tactile and gustatory sensibilities are closely intermingled in the substance of the mucous membrane. Thirdly, the sensibility of taste is not confined to the fibres of one special and distinct nerve, but resides in portions of two, namely, the lingual branch of the fifth pair and the glossopharyngeal nerve, which also supply general sensibility to the corresponding parts. Fourthly, this sense gives rise to impressions only from the actual contact of sapid substances with the mucous membrane, and can establish no communication with objects at a distance; and Fifthly, though some of the impressions derived from this source are of a distinct and special character, others, like the taste of oily or mucilaginous substances, differ but little in kind from those of tactile sensibility.

The sense of taste is localized in the mucous membrane of the tongue, the soft palate, and the pillars of the fauces. The tongue, which is more particularly the seat of this sense, is a flattened, leaf-like muscular organ, attached to the inner surface of the symphysis of the lower jaw in front, and to the os hyoides behind. It has a vertical sheet or lamina of fibrous tissue in the median line which serves as its framework, and is provided with longitudinal, transverse, and radiating muscular fibres, by which it can be elongated, retracted, and moved in every direction.

The mucous membrane of the fauces and posterior third of the tongue, like that lining the cavity of the mouth, is covered with vascular papillæ, analogous in structure to those of the skin, but imbedded and concealed in the smooth layer of epithelium forming the surface of the organ. Upon the dorsum of the tongue, about the junction of its posterior and middle thirds, there is a double row of rounded eminences, arranged in a V-shaped figure, running forward and outward, on each side, from the situation of the foramen cæcum; and from this point forward, the mucous membrane is covered with thickly-set papillæ, containing nerves and bloodvessels, and giving a soft velvety texture to the surface of the organ.

The lingual papillæ are of three different kinds. First the *filiform*

papillæ, which are the most numerous, and which cover most uniformly the upper surface of the tongue. They are long and slender, and are covered with horny epithelium, usually prolonged into filamentous tufts. At the edges of the tongue they are often united into parallel ranges or ridges of the mucous membrane. Secondly, the *fungiform papillæ.* These are thicker and larger than the foregoing, of a club-shaped figure, and covered with soft epithelium. They are most abundant at the tip of the tongue, but may be seen elsewhere on the surface of the organ, scattered among the filiform papillæ. Thirdly, the *circumvallate papillæ.* These are the rounded eminences, eight or ten in number, which form the V-shaped figure near the situation of the foramen cæcum. Each consists of a central eminence, surrounded by a wall or circumvallation, from which they derive their name. The circumvallation, as well as the central eminence, has a structure similar to that of the fungiform papillæ.

The sensitive nerves of the tongue, as above mentioned, are two in number, namely, the lingual branch of the fifth pair, and the lingual portion of the glossopharyngeal. The lingual branch of the fifth pair enters the tongue at the anterior border of the hyoglossal muscle. Its branches pass from below upward and from behind forward, between the

Fig. 187.

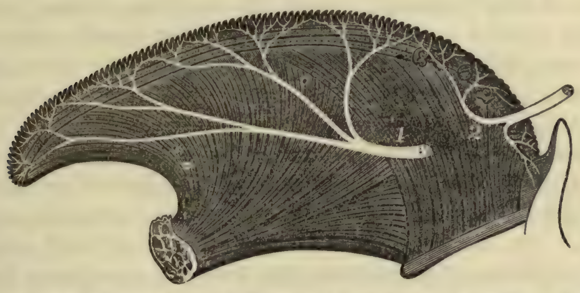


Diagram of the Tongue, with its sensitive nerves and papillæ.—1. Lingual branch of the fifth pair. 2. Glossopharyngeal nerve.

muscular bundles of the organ, until they reach its mucous membrane. The nerve fibres then penetrate the lingual papillæ, where they terminate, partly in the "terminal bulbs" already described (p. 594), and partly in a manner not yet distinctly ascertained.

The lingual portion of the glossopharyngeal nerve passes into the tongue below the posterior border of the hyoglossus muscle. It then divides into various branches, which pass through the muscular tissue, and are distributed to the mucous membrane of the base and sides of the organ.

The mucous membrane of the base of the tongue, of its edges, and of its under surface near the tip, as well as that of the mouth and fauces generally, is also supplied with mucous follicles furnishing a viscid

secretion by which its free surface is lubricated. The muscles of the tongue are animated exclusively by filaments of the hypoglossal nerve.

The *exact seat* of the sense of taste has been determined by placing in contact with different parts of the mucous membrane a small sponge, moistened with a solution of some sweet or bitter substance. The experiments of Dugès, Vernière, and Longet, have shown that taste resides in the whole superior surface, the point and edges of the tongue, the soft palate, fauces, and part of the pharynx. The base, tip, and edges of the tongue possess the greatest amount of sensibility to savors, the middle portion of its dorsum less, and its inferior surface little or none. As the whole anterior part of the organ is supplied by the lingual branch of the fifth pair alone, and the whole of its posterior portion by the glossopharyngeal, it follows that the sense of taste is derived from both these nerves.

Furthermore, the tongue is supplied, *at the same time and by the same nerves, with general sensibility and with the special sensibility of taste.* The general sensibility of the anterior portion of the tongue, and that of the branch of the fifth pair with which it is supplied, are sufficiently well known. Section of the fifth pair destroys the sensibility of this part of the tongue as well as that of the rest of the face. Longet found that after division of the lingual branch of this nerve, the mucous membrane of the anterior two-thirds of the tongue might be cauterized with a hot iron or with potassium hydrate in the living animal, without producing any sign of pain. Reid, on the other hand, determined that ordinary sensibility exists in a marked degree in the glossopharyngeal nerve, and is supplied by it to the parts in which its branches are distributed.

A distinction is to be made, in the action of foreign substances taken into the mouth, between the *special impressions derived from their sapid qualities*, and the *general sensations produced by their ordinary physical properties.* As the same substance is often capable of exciting both tactile and gustatory impressions, the two are sometimes liable to be confounded with each other. The truly sapid qualities, which we perceive by the special sense of taste, are savors, designated by the terms *sweet*, *bitter*, *salt*, *sour*, *alkaline*, and the like. Beside these, however, there are other characters, belonging to various articles of food, which partake largely of the nature of ordinary physical properties, appreciable by means of general sensibility. A *starchy*, *oily*, or *mucilaginous* taste, when uncomplicated with additional savors, is but little different in kind from the tactile impressions produced by the same substances. The quality of *pungency*, communicated to the food by the use of condiments, as pepper or mustard, is one which is appreciated altogether by the general sensibility. The *styptic* taste seems to be a combination of an ordinary astringent effect with a peculiar excitement of the gustatory nerves, analogous to that caused by the galvanic stimulus.

Furthermore, the taste or *savor* of a substance is to be distinguished from its odoriferous properties or *flavor.* In most aromatic articles of

food, such as tea and coffee, and the various kinds of wine, a great part of the effect produced is due to the aroma or smell which reaches the nares during the act of swallowing. Even in many kinds of solid food, such as freshly cooked meats, their odor takes a very important share in producing the impression on the senses. If, during the deglutition of such substances, the nares be compressed so as to suspend in great measure the sense of smell, their ordinary flavor becomes nearly imperceptible; and a similar effect is produced by catarrhal inflammation of the nasal passages, which suspends more or less completely the sensibility of the olfactory membrane.

Necessary Conditions of the Sense of Taste.—There are certain conditions requisite for the production of gustatory impressions, beside the integrity of the organ by which they are received.

In the first place, the sapid substance, in order that its taste may be perceived, must be brought in contact with the mucous membrane *in a state of solution.* So long as it remains solid, however marked a savor it may possess, it gives no other impression than that of a foreign body in contact with the tongue. But if applied in a liquid form, it spreads over the surface of the mucous membrane, and its taste is perceived. Thus it is only the liquid and soluble portions of the food which are tasted, such as the animal and vegetable juices and the soluble salts. Saline substances which are insoluble, such as calomel or lead carbonate, when applied to the tongue, produce no gustatory sensation.

The mechanism of the sense of taste is, in all probability, a direct and simple one. The sapid substances in solution penetrate the lingual papillæ by endosmosis, and, coming in contact with the terminal nervous filaments, excite their sensibility by uniting with the substance of which they are composed. The rapidity with which endosmosis will take place under certain conditions is sufficient to account for the instantaneous perception of sapid substances when introduced into the cavity of the mouth.

It is on this account that a *free secretion of the salivary fluids* is essential to the full performance of the gustatory function. If the mouth be dry and parched, the food seems to have but little taste. When the saliva, on the other hand, is freely secreted, it mixes readily with the food in mastication, and assists the solution of its sapid ingredients; and the fluids of the mouth, impregnated with the savory substances, are absorbed by the mucous membrane, and excite the gustatory nerves.

An important part is also taken in this process by the *movements of the tongue.* By these movements the food is carried from one part of the mouth to another, pressed against the hard palate, the gums, and the cheeks, its solution assisted, and the penetration of fluids into the papillæ more rapidly accomplished. If powdered sugar, or a bitter extract, be simply placed upon the dorsum of the tongue, little or no effect is produced; but when pressed by the tongue against the roof of the mouth, as in eating or drinking, its taste is immediately perceived.

This effect is easily explained; since it is well known how readily movement over a free surface, combined with slight friction, will facilitate the solution and imbibition of solid substances. The nervous papillæ of the tongue may therefore be regarded as the essential organs of taste, and the lingual muscles as its accessory organs.

Impressions of taste made upon the tongue *remain for a certain time afterward.* When a very sweet or a very bitter substance is taken into the mouth, its taste is retained for several seconds after it has been ejected or swallowed. Consequently, if several different savors be presented to the tongue in rapid succession, we become unable to distinguish them, and they produce only a confused impression, made up of the union of various different sensations. The taste of the first, remaining in the mouth, is mingled with that of the second, the taste of both with that of the third, and so on, until neither one can be distinguished. It is notoriously impossible to recognize several different kinds of wine with the eyes closed, if they be repeatedly tasted in quick succession.

If the substance first tasted have a particularly marked savor, its impression will preponderate over that of the others. This effect is especially produced by substances which excite the general sensibility of the tongue, such as acrid or stimulating powders; and it belongs, in the greatest degree, to substances which are at the same time sapid, pungent, and aromatic, like sweetmeats flavored with the volatile oils. Advantage is sometimes taken of this in the administration of disagreeable medicines. By first taking into the mouth some highly flavored and pungent substance, nauseous drugs may be swallowed immediately afterward with but little perception of their disagreeable qualities.

Sense of Smell.

The distinguishing character of the sense of smell is that it gives us intelligence of the physical quality of bodies in a *gaseous* or *vaporous* condition. Thus by its aid it is possible to detect the existence of an odoriferous substance at a distance, and although it may be concealed from sight. The minute quantity of volatile material emanating from it, and pervading the atmosphere, produces, by contact with the olfactory membrane, the special sensation of smell. The sense of smell differs, furthermore, from that of taste in being more distinctly localized. While the gustatory sensibility is distributed over the whole mucous membrane covering the dorsum and base of the tongue, and is supplied to its various parts by two different sensitive nerves, that of smell is confined to the upper portion of the nasal passages and is dependent on the filaments of a single special nerve.

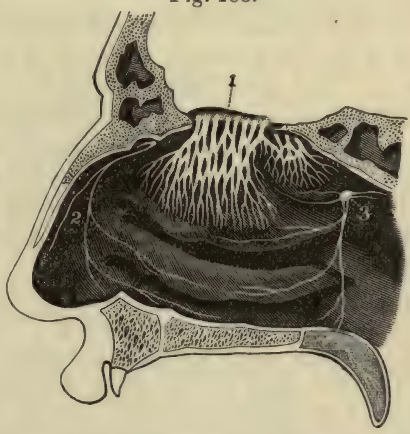
The mucous membrane covering the superior and middle turbinated bones and the upper part of the septum nasi, which is alone capable of receiving odorous impressions, and is limited by a tolerably well-defined outline, is known as the *olfactory membrane.* It is easily distinguishable from that of the rest of the nasal passages: 1st, by its color, which in man, the sheep, and the calf is yellow, but in most of the other mam-

malia has a brownish tinge; 2dly, in its softer and more succulent consistency; and 3dly, in the greater thickness, not only of the whole membrane but also of its epithelial layer. According to Kölliker, the epithelium of the olfactory membrane, in the sheep and the rabbit, is from 60 to 66 per cent. thicker than that of the remaining nasal mucous membrane. It also differs, according to the same observer, in the character of its surface. In most of the quadrupeds the epithelium of the Schneiderian mucous membrane generally is covered with vibrating cilia, which are absent in the olfactory portion; though in man the vibrating cilia may also be found in the epithelium of the olfactory portion itself. This difference of structure is probably connected with the inferior acuteness of the sense of smell in man, as compared with many of the lower animals.

The nasal passages are provided with nerves from three different sources.

I. The first and most important of these are the filaments of the *olfactory nerve* (Fig. 188, 1). They are derived immediately from the olfactory bulb, which rests upon the cribriform plate of the ethmoid bone, and from which they penetrate the nasal passages through the perforations in this bony lamina. An important peculiarity, however, shows itself in the nerve fibres of this region. While the substance of the so-called olfactory nerves within the cranial cavity, as well as that of the olfactory bulb, contains dark bordered medullated nerve fibres, like those in other parts of the white substance of the brain, the filaments which are given off from the under side of the olfactory bulb, and are distributed to the olfactory membrane, contain only pale, flattened, nucleated nerve-fibres without a medullary layer. The main question of interest in regard to them is that of their final mode of termination; but this, as in so many other similar cases, has thus far escaped absolute demonstration. The branches of the olfactory nerves frequently divide and subdivide, forming microscopic plexuses in the substance of the olfactory membrane; and the finest nervous ramifications are to be followed without doubt nearly to the epithelial surface of the membrane itself. According to the researches of Schultze, confirmed by these of Kölliker and Babuchin, the epithelium of this part

Fig. 188.



Distribution of Nerves in the Nasal Passages.—1. Olfactory bulb, with its nerves. 2. Nasal branch of the fifth pair. 3. Spheno-palatine ganglion.

consists of two different kinds of elongated cells, both standing vertically upon the mucous membrane, and closely adherent to each other by their lateral surfaces. One portion are analogous in form to ordinary nucleated columnar epithelium cells; the remainder are very slender and filamentous, except in their middle portion, at the situation of their oval nucleus. The deeper portion of these cells, which is also more slender than the rest, has been found to resemble the material of the nerve fibres in its reaction with solutions of gold chloride; but a direct continuity of substance between the fibres and the cells has not been shown in an unequivocal manner.

There is no doubt that the nerve filaments given off from the olfactory bulb are the special agents for communicating impressions of smell, and that they are the only ones endowed with olfactory sensibility. This follows from their exclusive and abundant distribution to the olfactory portion of the nasal membrane, from their comparatively large development in animals of acute smell, from the absence of this sense in cases of congenital absence of the olfactory bulbs, and from its loss in animals after their destruction (p. 515). So far as we can judge from the results of experiment, they are not capable of receiving or transmitting any other kind of sensibility than that excited by odoriferous substances.

II. The second set of nerves distributed to the nasal passages consists of the *nasal branch of the fifth pair*, and its ramifications (Fig. 188, 2). This nerve, after entering the cavity of the nose just in advance of the cribriform plate of the ethmoid bone, sends its filaments mainly to the mucous membrane covering the inferior turbinated bone and the walls of the inferior meatus, which are thus supplied with general sensibility, though they are destitute of the power of smell. Some filaments from this nerve, however, are also continued into the mucous membrane of the olfactory region, where they run in proximity to those of the olfactory nerves; and this region, according to the observations of Babuchin,[1] possesses consequently a certain amount of general sensibility, though much less than the remainder of the nasal passages.

III. The third set are those derived from the *spheno-palatine ganglion of the sympathetic* (Fig. 188, 3) which supply the mucous membrane of the posterior part of the nasal passages and the muscles aiding in the closure of the posterior nares. Finally, the muscles which regulate the expansion of the anterior nares are supplied by filaments of the facial nerve.

Necessary Conditions of the Sense of Smell.—In order to produce an olfactory impression, the emanations of the odoriferous body must be *drawn freely through the nasal passages.* As the sense of smell is situated only in the upper part of these passages, whenever an unusually faint or delicate odor is to be perceived, the air is forcibly directed toward the superior turbinated bones, by a peculiar inspiratory move-

[1] In Stricker's Manual of Histology, Buck's Edition. New York, 1872, p. 799.

ment of the nostrils, a movement which is very marked in many of the lower animals. As the odoriferous vapors arrive in the upper part of the nasal passages, they are probably dissolved in the secretions of the olfactory membrane, and thus brought into relation with its nerves. Inflammatory disorders consequently interfere with the sense of smell, both by altering the secretions of the part, and by producing a tumefaction of the mucous membrane, which prevents the free passage of air through the nasal fossæ.

A distinction is also to be made between the perception of true *odors*, and the excitement of the general sensibility of the Schneiderian mucous membrane by irritating substances. Some of the true odors are similar in their nature to impressions perceived by the sense of taste. Thus we have sweet and sour smells, though none corresponding to the alkaline or the bitter tastes. Most of the odors, however, are of a peculiar nature and are difficult to describe; but they are always distinct from the simply irritating properties which may belong to vapors as well as to liquids. Thus, pure alcohol has little or no odor, and is only stimulating to the mucous membrane; while the odor of wines, cordials, and perfumes, is communicated to them by other ingredients of a vegetable origin. The vapor of pure acetic acid is simply irritating; while vinegar has also a peculiar odor, derived from its vegetable constituents. Ammonia is an irritating gas, but contains no proper odoriferous principle.

The sensations of smell, like those of taste, *remain for a certain time* after they have been produced, and modify in this way other less strongly marked odors presented afterward. As a general rule, the longer the olfactory membrane is exposed to a particular odor, the longer its effect continues; and in some cases it may be perceived for many hours after the odoriferous substance has been removed. Odors, however, are particularly apt to remain after the removal or destruction of the source from which they were derived, owing to the facility with which they are entangled by porous substances, such as plastered walls, carpets, hangings, and woollen clothes.

The sense of smell, which is only moderately developed in the human species, is excessively acute in some of the lower animals. Thus, the dog will not only discover game and follow it by the scent, but will distinguish particular individuals by their odor, or recognize articles of dress belonging to them by the minute quantity of odoriferous vapor adhering to their substance.

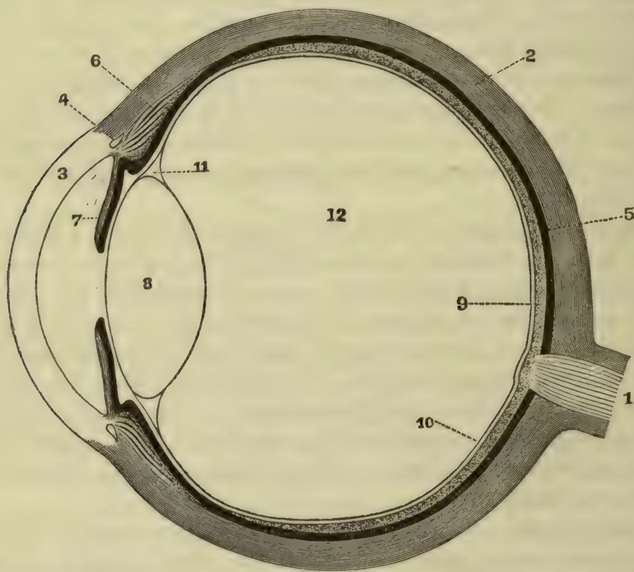
Sense of Sight.

This is the most remarkable of all the senses, both for the special nature of the impressions which it receives, the complicated structure of its apparatus, and the variety and value of the information which it affords with regard to external objects. It is by this sense that we receive the impressions of light and color, with all their modifications of intensity and combination, and acquire our principal ideas of form,

space, and movement. The organs of touch, taste, and smell, in order to perform their functions, must be placed in actual contact with the foreign substances which excite their activity; and even that of hearing is affected only by the sonorous vibrations of the atmosphere, or of some other solid or fluid medium. But the eye is equally sensitive to the impressions of light, whether it come from near or remote objects, or even from the immeasurable distances of the fixed stars. It is also superior to the other organs of special sense in the rapidity of its action, and in the delicacy of the distinctions which it is capable of making in the physical qualities of external objects; and it affords the most continuous and indispensable aid for all the ordinary occupations of life.

Organ of Vision.—The eyeball consists of a spheroidal fibrous sac, the *sclerotic coat* (Fig. 189, 2), filled with fluid and gelatinous material,

Fig. 189.



Horizontal Section of the Right Eyeball.—1. Optic nerve. 2. Sclerotic coat. 3. Cornea. 4. Canal of Schlemm. 5. Choroid coat. 6. Ciliary muscle. 7. Iris. 8. Crystalline lens. 9. Retina. 10. Hyaloid membrane. 11. Canal of Petit. 12. Vitreous body.

provided anteriorly with a transparent portion, the *cornea* (3), and lined at its posterior part with a nervous expansion, the *retina* (9), which is sensitive to light, and which receives the luminous rays admitted through the cornea. The cavity of the eyeball is therefore like that of a room with but one window, where all the light which enters from the front necessarily strikes the back wall of the apartment. There are, in addition to the above-mentioned parts, a transparent refracting body with convex surfaces, the *crystalline lens* (8), by which the light is

concentrated at the level of the retina; a perforated muscular curtain or diaphragm, the *iris* (7), placed in front of the lens, which regulates the quantity of light admitted through its central orifice, the pupil; and finally a vascular membrane with an opaque layer of blackish-brown pigment, the *choroid* (5), which lines the whole inner surface of the sclerotic and the posterior surface of the iris, thus preventing reflections within the eye, and absorbing all the light which has once passed through the substance of the retina. The construction of the eyeball, in its general arrangement as an organ of vision, is not unlike that of a photographic camera; where the sensitized plate at the back part represents the retina, the blackened inner surface of the box the choroid, while the lenses of the tube in front perform the office of the crystalline lens and cornea of the eyeball.

Sclerotic Coat.—The sclerotic, so named from its toughness and resistance, is the external coat and protective membrane of the eyeball. It is composed of condensed layers of connective tissue, similar to those of the fasciæ and membranous tendons in general; and toward its anterior third it receives the tendons of the external muscles of the eyeball, which become fused with its substance. Posteriorly it is continuous with the neurilemma of the optic nerve (Fig. 189, 1), which penetrates it from behind at its point of entrance into the eyeball. A portion of the sclerotic is visible anteriorly through the conjunctiva, forming the so-called "white" of the eye.

Cornea.—The cornea, which derives its name from its firm consistency and homogeneous appearance, resembling that of horn, forms the anterior part of the wall of the eyeball. It is inserted into the nearly circular space left at this situation by the deficiency of the sclerotic, with the texture of which it is continuous at its edges; the difference in the physical appearance of the two being that the sclerotic is white and opaque, while the cornea is colorless and transparent, so that the colored iris and dark pupil are visible through its substance. The surface of the cornea has a sharper curvature than that of the sclerotic, so that it projects from the front of the eyeball, like a smaller dome set upon a larger one. Its outline, where it joins the edge of the sclerotic, is a little oval in form, the transverse diameter of the cornea, in man, being slightly longer than the vertical. At its centre, it is about 0.8 millimetre in thickness, becoming a little thicker at its edges. Its anterior surface is kept polished and brilliant by the watery secretion of the lachrymal glands, distributed over it by the frequent movements of the eyeball and the lids.

At the outer border of the cornea, where it joins the sclerotic, and where the tissues of the two membranes pass into each other, there is a small cavity, running, in the form of a circular canal, the *canal of Schlemm* (Fig. 189, 4), through the thickness of this part of the wall of the eyeball. The inner wall of the canal of Schlemm is composed of elastic and tendinous tissue, and gives attachment to the fibres of the ciliary muscle on the one hand, and on the other to the outer border of

the iris. The canal itself is regarded by most anatomists as occupied by a venous plexus, which receives veins from the ciliary muscle and from the anterior part of the sclerotic.

Choroid.—The choroid coat is a vascular and pigmentary membrane, lining the inner surface of the sclerotic, and presenting anteriorly a thickened portion, the "ciliary body." The inner part of the ciliary body is thrown into a series of radiating folds, the "ciliary processes," which surround the borders of the crystalline lens. The internal surface of the choroid is occupied by a layer of hexagonal nucleated cells, closely packed side by side, and filled with granules of blackish-brown pigment. Similar pigment is also deposited, though less abundantly, in the substance and near the external surface of the choroid. At its anterior part, the choroid is separated from the internal surface of the sclerotic by the ciliary muscle (Fig. 189, 6). This muscle is composed of unstriped fibres, which arise from the inner wall of the canal of Schlemm, at the junction of the sclerotic and cornea, and thence diverge in a radiating direction, outward and backward, to be inserted into the external surface of the choroid, at the point where it begins to pass into the folds of the ciliary processes. At the anterior and inner part of the muscle there are also bundles of circular fibres, running parallel with the margin of the cornea. The whole muscle is thus composed of two parts; namely, an internal circular, and an external radiating portion, the fibres of which are more or less interwoven with each other at the inner edge of the muscular layer.

Iris.—The iris is a variously colored membrane, extending across the antero-posterior axis of the eyeball, attached by its external border to the inner wall of the canal of Schlemm, and presenting at its centre the nearly circular orifice of the pupil. It consists of connective and muscular tissue, with an abundant supply of bloodvessels, and is covered on its posterior surface by a layer of blackish-brown pigment cells, continuous with that of the choroid. The color of the iris, which appears, in different individuals, blue, gray, brown, or black, depends upon the abundance and disposition of its pigmentary elements. In gray and blue eyes, the visible hue of the iris depends upon the diffused light of its semi-transparent tissues, seen against the dark back-ground of the pigment layer upon its posterior surface. In brown and black eyes, the pigment is more abundant, and is deposited, according to Kölliker and Cruveilhier, not only upon the posterior aspect of the iris, but also in its stroma, between its fibres, and to some extent even upon its anterior surface. It thus predominates, and extinguishes more or less completely the reflected and diffused light of the remaining elements of the tissue.

The position of the iris is such that while its outer border is attached to the junction of the cornea and sclerotic, its central portion lies in contact with the anterior surface of the crystalline lens. According to the observations of Helmholtz,[1] the iris in myopic eyes is sometimes so

[1] Optique Physiologique, traduit par Javal et Klein. Paris, 1867, p. 20.

nearly flat that it throws no perceptible shadow under an extreme lateral illumination; but in normal eyes, as a rule, the portion immediately surrounding the pupil is sufficiently prominent to throw a distinct shadow; and if the source of illumination be not more than one millimetre in advance of the edge of the cornea, this shadow may extend even to the opposite border of the iris.

When the pupil dilates, the central prominence of the iris of course diminishes, or even disappears altogether; but, according to Helmholtz, the pupillary border of the iris hardly separates from the anterior face of the lens, even in the most complete dilatation obtainable by belladonna.

An important portion of the structure of the iris is formed by its muscular fibres. These are arranged in two sets, both of which consist of unstriped fibres, namely, the sphincter and the dilator muscles of the pupil.

The *sphincter pupillæ* is composed of bundles of muscular fibres, situated at the pupillary margin of the iris, and circularly disposed, in such a manner that their contraction has the effect of diminishing the orifice of the pupil, while their relaxation allows of its enlargement. When the sphincter is in a state of moderate contraction, the remaining non-contractile portions of the iris are thrown into radiating folds, which can be readily seen, under the influence of ordinary daylight, extending from the pupillary margin for one-third or one-half the distance toward its outer border.

The *dilator pupillæ*, which consists of radiating muscular fibres, is much more difficult of demonstration, and its existence in man continued to be a matter of uncertainty, even after it was known to be present in the lower animals. It has, however, been described by so many independent observers, that there can be no doubt of its forming a normal part of the muscular apparatus of the iris. Its fibres are interwoven with those of the sphincter at the pupillary margin, and extend thence in a diverging direction toward the attached border; either as isolated bundles running between the bloodvessels (Brücke, Kölliker), or as a very thin, continuous sheet of fibres, covering the whole posterior surface of the iris, immediately underneath its pigmentary layer (Henle, Iwanoff). According to Kölliker, the iris also contains elements analogous to the fibres of elastic tissue, which may thus assist the action of the dilator.

Notwithstanding the acknowledged existence of both these muscles, and their evident physiological association with each other, the action of the sphincter is much the most prominent and the most clearly understood. It is this muscle which contracts under the influence of light falling upon the retina, causing contraction of the pupil, and which relaxes when the stimulus is withdrawn, causing dilatation. The contraction of the pupil is therefore, for the most part, an active movement; its dilatation a passive one. Division of the oculomotorius nerve, loss of sensibility in the retina, opacity of the crystalline lens, or insensi-

bility from cerebral compression, are all followed by dilatation of the pupil; and the same thing takes place immediately after death. In the normal reflex actions of expansion and contraction of the pupil, under the varying intensity of illumination, the fibres of the sphincter are those which alternately contract and relax in a manner analogous to that of the voluntary muscles; while those of the dilator are more continuous in their operation, and are under the control of different nervous influences.

The pigmentary layer which is continued uninterruptedly, except at the entrance of the optic nerve, over the internal surface of the choroid, the ciliary processes, and the posterior surface of the iris, is called the system of the *uvea*, from its resemblance to the skin of a purple grape separated from its stem; the opening of the membranous sac at the point of detachment representing the orifice of the pupil. Owing to the existence of this continuous pigmentary layer, no light can penetrate the eyeball excepting that which enters through the pupil; and the rays, furthermore, which reach the retina at any point are arrested there, and prevented from being dispersed by reflection over other parts of the membrane.

Aqueous Humor and Vitreous Body.—By the transverse partition of the iris, the cavity of the eyeball is divided into two portions, an anterior and posterior. The portion situated in front of the iris, called the "anterior chamber," is filled with a colorless, transparent fluid, of watery consistency, the *aqueous humor.* This fluid is to be regarded as an extremely dilute exudation from the bloodvessels of the surrounding parts, especially from those of the iris; since it consists mainly of water, holding in solution less than two per cent. of solid ingredients, namely, sodium chloride and other inorganic salts derived from the blood, with a trace of albuminous matter. It is faintly alkaline in reaction, and has a refractive power but slightly different from that of water. It is rapidly reproduced after evacuation by puncture of the cornea. It serves to maintain the internal tension of the anterior parts of the eyeball, and to allow of the changes of figure of the iris and crystalline lens, without affecting the external configuration of the cornea. The posterior and larger portion of the cavity of the eyeball is filled mainly by a semifluid substance, *the vitreous body*, so called from its transparent and glassy appearance. Its composition is similar to that of the aqueous humor, excepting for the larger proportion of albuminous matter, which gives it more or less of a gelatinous consistency. Its refractive power, according to Helmholtz, though slightly greater than that of the aqueous humor, does not differ much from that of water. It distends the principal part of the cavity of the sclerotic, supports the retina which is extended over its surface, and preserves the general spheroidal form of the eyeball.

The vitreous body is enveloped by an exceedingly thin, colorless membrane, for the most part without definite structure, and measuring, according to Kölliker, not more than 4 mmm. in thickness. This is the

"hyaloid membrane" (Fig. 189, 10). Its inner surface is in contact with the vitreous body, its outer surface with the retina. It extends uninterruptedly over the posterior and middle portions of the vitreous body until it reaches a point anteriorly corresponding with the ciliary body of the choroid. Here it becomes thicker and divides into two layers. The anterior layer, which is the stronger of the two, the *zone of Zinn*, extends forward and inward, remaining adherent to the folds of the ciliary body, and terminates in the capsule of the crystalline lens, just in front of its lateral border. The posterior layer of the hyaloid membrane, after separating from the anterior, passes inward and a little backward, and terminates also in the capsule of the lens, but a little behind its lateral border. The triangular canal left between the two separated layers of the hyaloid membrane and the lateral border of the lens is the *canal of Petit* (Fig. 189, 11), and is filled with a little transparent serosity. The lens is thus suspended on all sides by a double layer derived from the hyaloid membrane. The anterior portion of this double layer, or the zone of Zinn, being the stronger of the two, and presenting a distinctly fibrillated texture, is regarded as more especially fulfilling the part of a suspensory ligament of the crystalline lens.

Crystalline Lens.—The lens is a transparent, refractive body, of circular form, with convex anterior and posterior surfaces, placed directly behind the pupil, and retained in its position by the counterbalancing pressure of the aqueous humor and the vitreous body, and by the two layers of the hyaloid membrane attached to its capsule round its circular border. It is composed of flattened fibres, adherent to each other by their adjacent surfaces and edges, and so arranged as to pass in a curvilinear direction, parallel to the surface of the lens, from one of its two opposite poles to the other. Notwithstanding the fibrous structure of the lens, the ribbon-shaped elements of which it is composed being united by simple juxtaposition, without the intervention of any different material, the entire body is transparent, and allows the passage of the light without perceptible absorption or irregular dispersion.

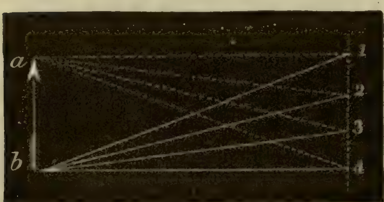
As the refractive power of the substance of the crystalline is greater than that of the cornea or the aqueous humor, it acts, by virtue of its double-convex form, as a converging lens, to change the direction of the luminous rays passing through it, and bring them to a focus at some point situated behind its posterior surface. The amount of convergence thus effected by a refractive lens depends both upon the index of refraction of the substance of which it is composed and the greater or less curvature of its surfaces. The stronger the curvatures, for lenses composed of the same material, the greater the amount of convergence impressed upon luminous rays passing through them. In the case of the crystalline lens of the human eye, the two surfaces are different in curvature; the anterior surface being comparatively flat, the posterior much more convex. According to the estimates of Listing, based upon a variety of measurements, and adopted by Helmholtz, the

radius of curvature for the anterior surface is, on the average, 10 millimetres, that for the posterior surface 6 millimetres.

This makes the crystalline lens the most powerfully refracting body in the eyeball, and by it said parallel or diverging luminous rays, after passing through the pupil, are brought to a focus at the situation of the retina. This effect is not due entirely to the lens, since the convex form of the cornea and the more or less spheroidal figure of the whole eyeball necessarily have in some degree a similar action upon rays entering from the front. According to Helmholtz, parallel rays would be brought to a focus by the cornea alone, if they were sufficiently prolonged, at a point situated 10 millimetres behind the retina. But on passing through the lens, their convergence is increased to such a degree that they are concentrated at the situation of the retina itself.

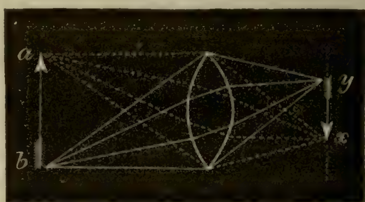
The function of the crystalline lens is to produce distinct perception of form and outline. If the eye consisted merely of a sensitive retina, covered with transparent integument, although the impressions of light would be received by such a retina, they could give no idea of the form of particular objects, but would only produce the sensation of a confused luminosity. This condition is illustrated in Fig. 190, where the arrow, *a*, *b*, represents the luminous object, and the vertical dotted line, at the right of the diagram, represents the retina. The rays, diverging from every point of the object in every direction, will thus reach every part of the retina. The different parts of the retina, consequently, 1, 2, 3, 4, will each receive rays coming both from the point of the arrow, *a*, and from its butt, *b*. There will, therefore, be no distinction, upon the retina, between the different parts of the object, and no definite perception of its figure. But if, between the object and the retina, there be inserted a double convex refracting lens, with the proper curvatures and density, as in Fig. 191, the effect will be different. All the rays emanating from

Fig. 190.



VISION WITHOUT A LENS.

Fig. 191.



VISION WITH A LENS.

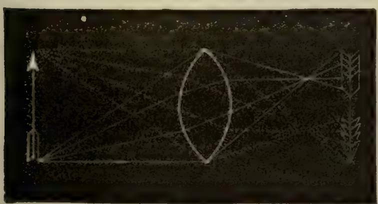
a will then be concentrated at *x*, and all those emanating from *b* will be concentrated at *y*. Thus the retina will receive the impression of the point of the arrow separate from that of its butt; and all parts of the object, in like manner, will be distinctly and accurately perceived.

The action of a refractive body with convex surfaces, in thus focussing luminous rays at a particular point, may be readily illustrated in the following manner. If a sheet of white paper be held at a short distance from a candle flame, in a room where there is no other source of light,

the whole of the paper will be moderately and uniformly illuminated by the diverging rays. But if a double convex glass lens, with suitable curvatures, be interposed between the paper and the light, the outer portions of the paper will become darker and its central portion brighter, because a portion of the rays are diverted from their original course and bent inward toward each other. By varying the position of the lens and its distance from the paper, a point will at last be found, where none of the light reaches the external parts of the sheet, but all of it is concentrated upon a single spot; and at this spot will be seen a distinct inverted image of the end of the candle and its flame.

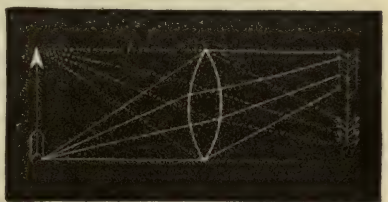
Distinct perception of the figure of external objects thus depends upon the action of the crystalline lens in converging all the rays of light, emanating from a given point, to an accurate focus at the retina. For this purpose, the density of the lens, the curvature of its surfaces, and its distance from the retina, must all be properly adapted to each other. If the lens were too convex, and its refractive power excessive, or if its distance from the retina were too great, the rays would converge to a focus too soon, and would not reach the retina until after they had crossed each other and become partially dispersed, as in Fig. 192. The visual impression, therefore, coming from any particular point in the object, would not be concentrated and distinct, but diffused and dim, from being dispersed more or less over the retina, and interfering with the impressions from other parts. On the other hand, if the lens were too flat, as in Fig. 193, or placed too near the retina, the rays

Fig. 192.



INDISTINCT IMAGE from excessive refraction.

Fig. 193.



INDISTINCT IMAGE from deficient refraction.

would fail to come together at all, and would strike the retina separately, producing a confused image, as before. In both these cases, the immediate cause of the confusion of sight is the same, namely, that rays coming from the same point of the object strike different points of the retina; but in the first instance, this is because the rays have actually converged and crossed each other; in the second, it is because they have only approximated, but have never converged to a focus.

The proof that the rays emanating from luminous objects are actually thus concentrated, in the interior of the living eye, upon the retina, is furnished by the use of the ophthalmoscope. This instrument consists essentially of a mirror, so placed as to illuminate by reflected light, through the pupil, the bottom of the eye which is under observa-

tion, and perforated at its centre by a small opening through which the observer looks. By this means the retina and its vessels, as well as the images delineated upon it, may be distinctly seen. According to the observations of Helmholtz, objects at a certain distance, which are perceived with distinctness, present to the eye of the observer, if sufficiently illuminated, perfectly well-defined inverted images upon the retina, like those which would be thrown upon a screen by a system of glass lenses properly arranged. If the eyeball furthermore be taken out from a recently killed animal, and a circular portion of the sclerotic and choroid removed from its posterior part, similar inverted images of illuminated objects in front of the cornea may be seen by transparency upon the exposed portion of the retina.

It is accordingly certain that luminous rays in passing through the eyeball are brought to a focus at the retina, principally by means of the crystalline lens. The formation of a visible image at this spot does not by itself explain all the phenomena of vision, since these images are not seen by the individual, and we should not even know of their existence except for the results of physiological experiment and observation. But the formation of such an image shows that all the light coming from each different part of the object is made to fall upon a separate and distinct point of the retina; and it thus becomes possible to perceive the figure and extension of an object, as well as its luminosity.

Retina.—The retina is the most essential part of the organ of vision, since it is the only one of its tissues directly sensitive to light. It forms a delicate, colorless, nearly transparent membrane, composed of nervous elements, situated between the inner surface of the choroid and the outer surface of the hyaloid membrane, and extending from the entrance of the optic nerve outward and forward to the commencement of the ciliary body. Here it terminates by an indented border, termed the *ora serrata*, which is situated nearly at the plane of the posterior surface of the crystalline lens. In front of this region it is replaced by an attenuated layer, which remains in contact with the surface of the ciliary body, but which contains no nervous elements. The retina proper has, accordingly, the form of a thin membrane moulded upon a nearly hemispherical surface, the concavity of which is directed forward, and which receives the luminous rays admitted through the pupil, and traversing the transparent and refracting media of the eyeball. Its greatest thickness is in the immediate vicinity of the entrance of the optic nerve, where it measures, according to Kölliker, 0.40 millimetre. At a short distance from this point it is reduced to 0.20, and thence becomes gradually thinner in its middle and anterior portions. At its terminal border, at the ora serrata, it is only 0.09 millimetre in thickness.

The retina consists of a variety of superimposed layers, in which many different microscopic elements alternate with each other. In regard to its physiological properties, so far as these have been determined with a sufficient degree of certainty, four of these layers may be distinguished as representing the essential constituent parts of the

membrane. These layers, counting from the internal to the external surface of the retina, are as follows: 1. The layer of nerve fibres, derived from the expansion of the optic nerve; 2. The ganglionic layer of nerve cells; 3. The layer of nuclei; 4. The layer of rods and cones.

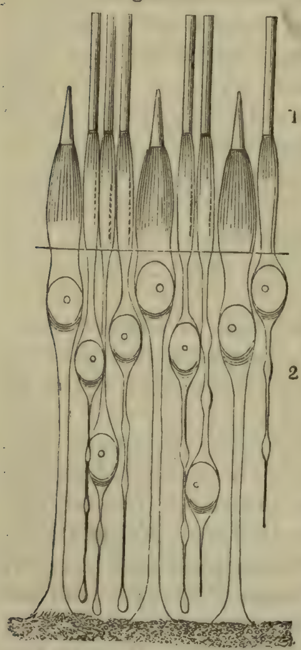
1. *Layer of Nerve Fibres.*—The optic nerve joins the posterior part of the eyeball at a point about 2 millimetres inside its longitudinal axis, and slightly below the horizontal plane of this axis. The neurilemma of the nerve at once becomes continuous with the sclerotic coat of the eyeball, while the nerve fibres alone penetrate into its cavity. Up to this point the fibres of the optic nerve present the usual dark-bordered appearance of medullated nerve fibres, and have, according to Kölliker, a diameter of from 1 to 4.5 mmm. But at their entrance into the cavity of the eyeball the nerve fibres not only lose the prolongations of connective tissue which previously surrounded their different bundles, but also become much smaller in size, being reduced, on the average, to less than 2 mmm., and many of them to less than 1 mmm. in diameter. Owing to these changes, the nerve appears suddenly diminished in size at its passage through the sclerotic and choroid membranes. Internally it forms a slight prominence on the inner surface of the wall of the eyeball, the so-called *papilla;* and from a depression at its middle part, the central artery and vein of the retina send out their branches to supply the retinal capillary plexus. From the papilla as a centre the optic nerve fibres, which have thus reached the inner surface of the retina, diverge in every direction under the form of a closely set layer. This layer diminishes gradually in thickness from within outward, and from behind forward, owing to the fact that the nerve fibres of which it is composed terminate successively in the deeper parts of the membrane, thus establishing a connection between every point of the retina and the nervous centres in the brain. The longest fibres continue their course until they reach the ora serrata at the anterior limit of the retina, beyond which none are visible.

2. *Ganglionic Layer of Nerve Cells.*—This layer is situated immediately outside the former, and contains, as its special distinguishing element, multipolar nerve cells, similar to those of the gray matter of the brain. According to Kölliker, they vary in size from 9 to 36 mmm. in diameter, and are provided with a number of pale, ramified prolongations. Some of these prolongations are directed outward, penetrating into the more external portions of the retina; others pass in a horizontal direction, and, according to some observers (Kölliker, Müller, Corti), become connected with optic nerve fibres. For the most part, however, it is only the identity in appearance between some of the prolongations of these nerve cells and the more slender optic nerve fibres, which leads to the presumption of their direct terminal continuity. It is, in any case, possible that some of the fibres of expansion of the optic nerve are connected with prolongations of the nerve cells, while others continue their course to the deeper layers of the retinal tissue.

3. *Layer of Nuclei.*—The layer of nuclei is so called because its most characteristic elements have, in the main, the aspect of nuclei; although by some observers (Kölliker, Schultze), they are regarded as having rather the signification of nucleated cells, in which the enveloping cell-substance is in small quantity as compared with the size of the nucleus. The nuclei themselves, sometimes called "grains" or "granules," are oval bodies, placed with their long axes perpendicular to the surface of the retina. There are two varieties of them mingled together, which differ mainly in size; the larger being from 9 to 13 mmm. in length, the smaller one-half or two-thirds as long. They are all contained in the interior of varicose enlargements of slender fibres, which are also directed perpendicularly to the surface of the retina, and extend uninterruptedly through the whole thickness of the layer. These fibres are presumed to be of the nature of modified nerve fibres, and to represent, either directly or indirectly, the continuations of those derived from the expansion of the optic nerve. At their outer extremities they are immediately continuous with the elements of the following layer.

4. *Layer of Rods and Cones.*—This is undoubtedly the most remarkable of the retinal layers, since it consists of elements which are more peculiarly constituted than those found elsewhere, and which are most immediately connected with the physiology of luminous impressions. As the name indicates, these elements are of two kinds; distinguished, according to their shape, by the name of "rods" and "cones." There is reason to believe that their offices are essentially similar, and that they are to be regarded as modifications of each other.

Fig. 194.



DIAGRAMMATIC SECTION, from the posterior portion of the human retina.—1. Layer of rods and cones. 2. Layer of nuclei. (Schultze.)

The *rods* (Fig. 194) are straight, elongated, cylindrical bodies, composed of a transparent, homogeneous substance, remarkable for its highly refractive power. They are about 50 mmm. in length by a little less than 2 mmm. in diameter. They are all placed parallel with each other, closely packed side by side, standing perpendicularly to the surface of the retina, and extending through the whole thickness of the layer. At its outer extremity each rod terminates by a plane perpendicular to its axis; at its inner extremity it tapers suddenly to a point and is continuous with a fibre of the preceding layer, and thus with one of its nucleated enlargements or grains. According to Schultze, the internal half of each rod is slightly thicker, and exhibits rather less refractive power than its external half.

The *cones* differ from the rods mainly in their tapering form and the greater diameter of their internal portion, which, as a general rule, is from two to three times as thick as that of the rods. They have the same transparent, highly refractive appearance, and are intercalated among the rods in the same position, that is, perpendicularly to the surface of the retina. Their outer extremities, in some regions, stop short of the external surface of the retina, while in others, particularly in that of most perfect vision, they reach the same level with the ends of the rods. Each cone is connected at its inner extremity with a nucleated fibre belonging to the preceding layer, the only difference in this respect being that both the fibres and the nuclei connected with the cones are larger than those connected with the rods.

Over the greater part of the retina the rods are more abundant than the cones. When viewed from the external surface (Fig. 195, *A*), their closely packed extremities present the appearance of a fine mosaic pattern, while the cones are interspersed among them in smaller numbers. At the borders of the macula lutea (p. 623), on the other hand, the cones are more abundant, being only separated from each other by single ranges of rods (*B*); and at its central portion (*C*) there are only cones, the rods being entirely absent. The cones at this point are also longer and more slender than elsewhere. The following figure indicates the appearance of the rods and cones, as shown in an external view of different parts of the retina. The smaller circles represent the rods, the larger circles the cones. In the interior of each cone is seen the section of its conical extremity.

Fig. 195.

OUTER SURFACE OF THE RETINA, showing the ends of the rods and cones.—*A*. From the lateral portion of the eyeball. *B*. From the posterior portion, at the edge of the macula lutea. *C*. From the macula lutea. (Helmholtz.)

Beside the distinctly marked layers above described, there are various others of less certain signification and less uniformity of extent, which are found in different parts of the retina. Throughout the membrane there also exists a certain proportion of delicate connective tissue, which serves for the support and attachment of its remaining anatomical elements.

Perception of Luminous Impressions by the Retina.—It appears, from the description given above, that the retina is not simply an expansion of the fibres of the optic nerve. It is a membrane of special structure, connected with the extremities of the optic nerve fibres, but containing also many additional anatomical elements. It is accordingly a peculiar nervous apparatus, adapted to receive the impression of luminous rays, and connected, by means of the optic nerve, with the central

gray matter of the brain. An examination of the manner in which the impressions of light are perceived brings into view the following facts.

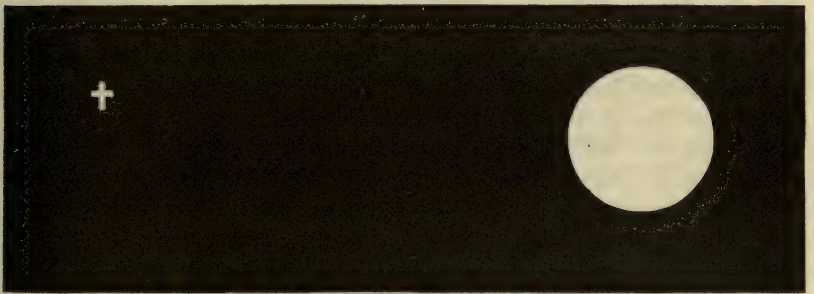
The optic nerve and its fibres are insensible to light. Notwithstanding that this nerve is capable of transmitting luminous impressions from the retina to the brain, yet in order to do this, it must first receive its own stimulus from the retina. The optic nerve fibres themselves, though sensitive to mechanical or galvanic irritation, cannot be called into activity by the direct influence of luminous rays. This is shown by the experiment of Donders, in which, by aid of the ophthalmoscope, a light of a certain degree of intensity is concentrated upon the optic nerve, without being allowed to reach the tissue of the retina. When the bottom of the eye is illuminated by the ophthalmoscope, the observer sees the general surface of the retina of a red or brownish color, while the *papilla*, which corresponds to the entrance of the optic nerve, presents itself as a white circular spot. This spot is occupied entirely by optic nerve fibres, while the elements of the retina commence only beyond its borders. If the minute image of a candle flame at some distance be thrown by reflection upon the retina, its light is perceived by the person under observation, as well as its image by the observer. If the eye however be turned in such a direction as to bring the image of the flame upon the white circle of the optic nerve, this circle, and the nerve fibres of which it is composed, are visibly illuminated to a certain depth, owing to the translucency of their substance; but the light of the candle flame is no longer perceived by the person under examination. The moment, on the other hand, the image of the flame is allowed to pass beyond the limits of the white spot, and to touch the retina, its light becomes perceptible.

The Blind Spot.—The region, accordingly, occupied by the entrance of the optic nerve, and in which the elements of the retina proper are absent, is a blind spot, where luminous rays make no perceptible impression. The real diameter of this spot, according to the average measurements obtained by Listing, Hannover, and Helmholtz, is 1.65 millimetre, and it covers in the field of vision a space equivalent to about 6 degrees. Notwithstanding the existence of this insensible part at the bottom of the eye, no dark point is usually observed in the field of vision, for the following reasons. The blind spot is not situated in the visual axis of the eye, but is placed, corresponding with the entrance of the optic nerve, nearer the median line (Fig. 189). Consequently the image of an object which is directly examined in the normal line of vision cannot fall upon this spot, but is always outside of it, at the end of the visual axis. Even an object which is perceived in the field of vision outside the direct line of sight, can never reach the blind spot of both eyes at the same time. If it happen to be so placed that its image falls upon the blind spot of one eye, it will necessarily reach the retina of the other eye at a different point, and is accordingly perceived. If, on the other hand, one eye alone be employed, there is always a small portion of the field of vision which is imperceptible. This deficiency is not generally

noticeable, because it is located in a part of the field to which our attention is not directed, and where the distinction of various objects, under moderate illumination, is so imperfect, that the momentary absence of one of them is not regarded. It may, however, be readily made apparent by using for the test a single strongly defined object, like a white spot on a black ground, the presence or absence of which may be noticed without difficulty, even in indirect vision.

If the left eye be covered and the right eye directed steadily at the white cross in figure 196, the circular spot will also be visible, though

Fig. 196.



DIAGRAM, for observing the situation of the blind spot. (Helmholtz.)

less distinctly, since it will be out of the direct line of sight. Let the page be held vertically at the height of the eyes, and at a convenient distance for seeing both objects in the above manner. If it be now moved slowly backward and forward, a point will be found where the circular spot disappears from sight, because its image has fallen upon the blind spot; while both within and beyond this distance it again becomes visible. It may also be made to reappear, even at the same distance, by inclining the page laterally to the right or left; since this brings the white circle either above or below the level of the blind spot.

The experiment may be varied by fixing two cards, at the height of the eyes, upon a dark wall, two feet apart from each other. If the left eye be covered, and the right eye fixed upon the left-hand card, the other one will disappear from view at a distance of about eight feet from the wall.

It is evident, furthermore, that the optic nerve fibres are not directly sensitive to light, even outside the blind spot, and where they form part of the retina. These fibres radiate from the point of entrance of the optic nerve, forming a continuous sheet on the inner surface of the retina; some of them terminating at successive points in the retinal membrane, others extending to its extreme border at the ora serrata. A luminous ray striking the retina near the fundus of the eye must, therefore, traverse a considerable number of nerve fibres, which are connected at their peripheral extremities with different parts of the retina; and such a ray, coming from a single point, would necessarily cause the sensation of multiplied luminous points or even of a more or less con-

tinuous bright line. As distinct points are actually perceived as such by the retina, although the luminous ray emanating from each one has passed through the whole layer of nerve fibres on its internal surface, it follows that the sensibility of these fibres is not affected by the direct action of light.

The sensitive elements of the retina are in its posterior or external layers. This fact is deduced partly from the phenomena manifested when the retinal bloodvessels are made visible in the interior of the eye. These bloodvessels and their branches radiate from the central trunk which enters with the optic nerve. Their ramifications, down to a certain size, are all situated in the nerve fibre layer of the retina, and it is only the finest subdivisions which pass into the next layer of ganglionic nerve cells. The two outer layers, namely, the layer of nuclei, and that of the rods and cones, are completely destitute of bloodvessels. Owing to this anatomical arrangement, the posterior or external layers of the retina, situated behind the main branches of the retinal bloodvessels, must lie in the shadow of these branches, the light coming directly from the front through the pupil. The shadows thus thrown are not habitually perceived by any diminution of the light, because the portions of the retina covered by them are always in shadow at the same points, and its sensibility to light is greater, in proportion as the quantity of light reaching it is less. But the shadows may be rendered perceptible by a lateral or oblique illumination, thus causing them to be thrown upon points of the retina unaccustomed to their presence.

Let a lighted candle be held, in a dark room, about three inches distant from the external angle of either eye, and about 45 degrees in advance of the plane of the iris. On moving the candle alternately upward and downward, the field of vision becomes filled with an abundant and elegant tracery of aborescent bloodvessels, the exact counterpart of those of the retina. The form of the vessels is distinctly marked in purple-black, upon a finely granular grayish-red ground. The point of entrance of the vascular trunks may even be seen, with their division into two principal branches passing respectively upward and downward, and then breaking up into ramifications of various curvilinear form. If the candle be held immovable, the appearances rapidly fade, since the shadows in reality are quite faint, and are only made visible from the sudden contrast produced by throwing them successively upon different parts of the retina.

As the bloodvessels which throw these shadows are at or near the anterior surface of the retina, the extent of their apparent movement on varying the position of the light, gives a means of ascertaining how far behind the anterior surface of the retina its sensitive elements are situated. According to the measurements of Müller,[1] this distance must be, in various cases, from 0.17 to 0.36 millimetre; and the same observer finds the posterior layers of the retina to be separated from its

[1] Cited in Helmholtz, Optique Physiologique. Paris, 1867, p. 289.

anterior surface by from 0.20 to 0.30 millimetre's distance. It is, therefore, one or both of the posterior layers, namely, that of the rods and cones, and that of the nuclei immediately within it, which contain the sensitive elements of the retina, and in which the luminous rays produce their effect. This conclusion is rendered still more certain by the fact that in the fovea centralis, the point of most distinct vision, hereafter to be described, the two external layers of the retina are the only ones present.

Macula Lutea and Point of Distinct Vision.—The macula lutea, or yellow spot of the retina, is an oval spot, measuring about 2 millimetres in its horizontal diameter, situated between 2 and 2.5 millimetres outside the entrance of the optic nerve. According to Helmholtz, it is placed a very little beyond the middle of the fundus of the eyeball, toward the temporal side. It is distinguished from the remainder of the retina by its yellow tinge, which depends upon the presence of a peculiar organic pigment. This pigment is not deposited in grains, but is completely hyaline, and imbibes the whole tissue of the retina at this spot, with the exception, according to Schultze, of the two external layers, which remain colorless.

At its centre is a minute depression, the *fovea centralis*, where, owing to its steeply sloping sides, the retina is reduced, at the bottom of the fovea, to less than one-half its usual thickness. The macula lutea becomes perceptible, in ophthalmoscopic examination of the eye with a moderate illumination, as a yellowish spot, less brilliant than the rest, in which the position of the fovea centralis is marked by a peculiar colorless reflection. The macula lutea, and especially the fovea centralis, *is the point of most distinct vision*, where the image of an object, fixed by the eye in the direct line of sight, falls upon the retina. It is well known that external objects are seen with perfect distinctness only when their images fall in the immediate neighborhood of the optical axis at the fundus of the eyeball. Outside this region, the perception of their figure is more or less imperfect. According to the observations of Donders, confirmed by Helmholtz, if, while the retina is illuminated by the ophthalmoscope, the person under observation fixes the eye in succession upon several different objects, or upon different points of the same object, the minute reflection which marks the fovea centralis always places itself upon the part of the optical image fixed by the eye; and this appearance is so constant that the observer can tell with certainty, from the place occupied by the reflection, what point of the object has been fixed in the direct line of sight.

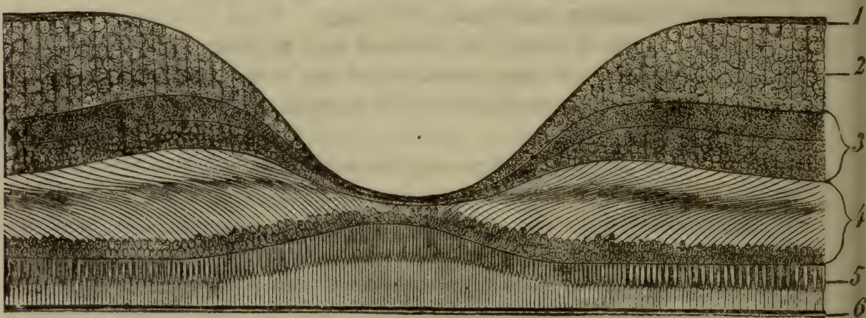
The evident importance of the macula lutea and the fovea centralis, in the exercise of vision, gives a special interest to the anatomical structure of this part of the retina; and the researches of microscopic anatomists have shown that its structure presents peculiarities fully corresponding with its physiological endowments.

The macula lutea is distinguished, in the first place, by the fact that *the superficial layer of optic nerve fibres is absent.* Those fibres, ac-

cording to Kölliker, which, in radiating from the entrance of the optic nerve, pass directly to the edges of the macula, lose themselves among the nerve cells of its ganglionic layer. The others curve round the borders of the macula on each side, to resume their peripheral direction beyond its limit; so that the yellow spot itself is not covered, like the rest of the retina, by a continuous superficial layer of nerve fibres.

Secondly, the nerve cells of the ganglionic layer are more abundant in the macula lutea than elsewhere. Over the greater portion of the retina, according to Schultze, these cells exist, in the ganglionic layer, only in a single plane; that is, they are arranged side by side, and neither above nor below each other. But in the yellow spot they form several ranges of superimposed cells. On the other hand, toward the centre of the yellow spot the cells diminish in number, and are entirely absent at the fovea centralis. Various other layers, which exist more or less distinctly in surrounding regions of the retina, also diminish in thickness, and disappear toward the centre of the macula lutea.

Fig. 197.



Diagrammatic Section of Human Retina, through the macula lutea and fovea centralis.—1. Internal surface of the retina, in contact with the vitreous body. 2. Ganglionic layer of nerve cells. 3. Intermediate layers of the retina, disappearing at the centre of the macula lutea. 4. Layer of nuclei, showing the oblique course of the fibres in this region. 5. Layer of rods and cones; consisting at its central portion exclusively of attenuated and elongated cones. 6. External surface of the retina, in contact with the choroid. In the middle of the diagram is the depression of the fovea centralis. (Schultze.)

Thirdly, owing to the modifications described above, the retina, at the situation of the fovea centralis, *consists only of its two external layers*, namely the layer of nuclei and the layer of rods and cones. Even these two layers exhibit, at this point, certain important peculiarities in the form and arrangement of their elements.

In the layer of nuclei, the nuclei themselves are present in nearly their usual numbers and position; but the fibres with which they are connected, instead of passing through the layer in a direction perpendicular to the surface of the retina, bend obliquely outward, to reach the more superficial layers of the retina in the external portions, or even beyond the borders, of the yellow spot. Thus this layer is very much diminished in thickness, although it still contains its cell nuclei,

and although these are still connected, by their fibrous extensions, with the other parts of the retinal tissue.

Finally the layer of rods and cones, at the situation of the macula lutea and fovea, though preserving its general character, shows special features by which it is readily distinguished from the corresponding parts elsewhere. In this layer, over the greater portion of the retina, the rods are the most abundant element, the cones being distributed among them in smaller numbers. In the borders of the macula lutea (Fig. 195, *B*), the cones become more numerous in proportion to the rods, and in the fovea centralis (Fig. 195, *C*) the layer is composed exclusively of cones. At this part, the cones are longer than elsewhere, and more slender, so that a larger number are comprised within an equal space; and the layer itself, consisting of elongated cones standing perpendicularly, is increased in thickness, in proportion to the greater length of its constituent elements. The thickness of the cones at their base, over the retina generally, according to the measurements of Schultze, is a little over 6 mmm., and their length less than 50 mmm.; but at the fovea centralis their thickness is reduced to 3 or 3.5 mmm., while their length, in the same situation, may reach 100 mmm. Each cone is connected, here as elsewhere, through the nucleus and nucleus fibre of the preceding layer, with the other portions of the retina, and beyond doubt, in some direct or indirect way, with the optic nerve fibres of its internal layer.

Thus the perception of light, in the act of vision, is a process consisting of several successive acts. The luminous ray passes through the transparent internal or superficial layers of the retina, until it reaches the situation of the two outer layers. Here it produces a change in the condition of the nervous elements, of whose nature we are entirely ignorant. It might be compared with that which is caused by the same agent in the sensitive film of a photographic camera; but this comparison would be only one of analogy, and would not imply any identity of the physical or chemical change produced in the two cases. It would simply express the fact, which is undoubtedly established, that the luminous ray, after traversing all the other transparent and refracting media of the eye without leaving any trace of its passage, on arriving at the two outer layers of the retina, excites in one or both of them a kind of action which is the first step in the visual process. This condition of the retinal elements then calls into activity the fibres of the optic nerve, which in turn transmit the stimulus to their point of origin in the brain. Thus far, there is no conscious perception, nor even any nervous effect resembling in itself our idea of luminosity. The retina itself is distinguished from other nervous tissues by being sensitive to light; that is, it may be thrown into a state of activity under the influence of a luminous ray. But it has no other *perception* of light than this, any more than the silvered film of a photographic plate; and, if the optic nerve be severed, blindness results, however perfect may be the condition of the retina.

On the other hand, the optic nerve fibres, which are insensible to light itself, are thrown into excitement by the changed condition of the retinal tissue. There is no reason for believing that the action of the fibres of the optic nerve is different in kind from that of other sensitive nerve fibres. Their office is simply that of receiving and communicating a stimulus from and to certain special structures containing nerve cells. In the case of the optic nerve, the stimulus is received from the retina and communicated to the nervous centres of the brain. These nervous centres, when excited by the stimulus thus received, first produce the phenomenon of the perception of *light*. The preceding nervous actions, in the retina and optic nerve, though necessary to the final result, have no direct connection with consciousness. The conscious perception of light and of luminous objects is the last step in the process of vision, and is effected by a special act of the gray matter of the brain.

Acuteness of Vision in the Retina.—The acuteness of vision, so far as it is connected with the sensibility of the retina, depends upon the minimum distance from each other of two visual rays, at which they can still be perceived as distinct points. If the luminous rays, coming respectively from the top and bottom of an object, are so closely approximated, where they strike the retina, that the two impressions are confounded, there can be no distinct perception of its figure or dimensions. On the other hand, if the sensibility of the retina be such that the two impressions are still perceived as separate from each other, the form of the object will be recognized as well as its luminosity, notwithstanding the small size of its retinal image. The figure of a man, six feet high, seen at the distance of ten yards, makes at the cornea a visual angle of 11° 30′, and forms upon the retina an image which is less than half a millimetre ($\frac{1}{50}$ of an inch) in length; and yet an abundance of details are distinctly perceptible within this space. The extreme limit of approximation at which two points may be distinguished from each other has been examined by the observation of fixed stars, and by that of parallel threads of the spider's web, or of fine metallic wires, placed at known distances from each other.[1] The general result of these examinations has shown that, for the average of well-formed eyes, the smallest visual angle, at which two adjacent points or lines can be distinguished, is from 60 to 73 seconds; corresponding to a distance upon the retina of from 4 to 5 mmm. According to the measurements of Schultze, the diameter of the retinal cones, at the fovea centralis, is from 3 to 3.5 mmm.; and if two points of light were separated at the retina by a less distance than this, they would often fall upon the same cone, and consequently excite the same nucleus and fibre in the adjacent layer. If the diameter of the cones be the element which determines the limit of acuteness of vision, two luminous points, to be distinctly perceptible, must be separated upon the retina by a distance of at least 3 mmm., and must have a visual angle with each other of at least 42

[1] Helmholtz, Optique Physiologique. Paris, 1867, p. 292.

seconds. In the observations made upon fixed stars, it is found that two stars can never be separately distinguished by the eye unless their angular distance from each other is equal to 30 seconds; and very seldom, unless it be as great as 60 seconds. These measurements correspond with each other only in an approximative manner; perhaps because there has never been an opportunity of examining the retinal elements in an eye, of which the acuteness of vision has been tested beforehand. But they are sufficient to indicate a probable connection between the minute structure of the retina and the possible limit of its sensibility to separate impressions.

Physiological Conditions of the Sense of Sight.—The apparatus of vision, as above described, consists of various parts, each of which has its appropriate share in producing the final result of visual perceptions. The eye, so far as regards its physical structure, is an optical instrument, composed of transparent and refracting media, a perforated diaphragm, and a dark chamber lined with a blackened membrane, all of which act upon the luminous rays according to the same laws as the corresponding parts in a telescope or a camera; and the accuracy of their adjustment is one of the first requisites for the exercise of sight. The organ, furthermore, is movable as a whole; and certain of its internal parts are also under the control of muscular tissues, whose alternate contraction and dilatation contribute to determine its mode of action. It is, in addition, a double organ; and impressions may be derived from the simultaneous employment of both eyes, which cannot be acquired by the use of one alone. Finally, the special sensibility of its nervous elements is liable to modifications of various kinds, which have an influence upon the nature and intensity of the sensations produced. The principal conditions regulating the physiological exercise of the sense of sight are the following:

Field of Vision.—As the eyeball is placed in the orbit with the cornea and the pupil directed forward, there is, in front of each eye, a circular space within which luminous objects are perceptible; while beyond its borders, laterally and posteriorly, nothing can be seen. This space is the "field of vision." Its extreme limit, in man, reaches nearly to 180 degrees of angular distance; that is to say, with the eye directed straight forward, the light from a brilliant object may be perceived, when the object itself is placed laterally almost as far back as the plane of the iris. The possibility, for light which has come from this direction, of penetrating the pupil and finally reaching a sensitive part of the retina, depends upon the refractive power of the cornea and the curvature of its anterior surface, by which the luminous ray is bent inward and thus enabled to enter obliquely the orifice of the pupil. In many of the lower animals, where the eyes are more prominent than in man, and the curvatures of the cornea and crystalline lens more pronounced, the field of vision is enlarged in a corresponding degree. In birds and fishes, it is still further modified by the lateral

position of the two eyes. The ostrich, with the head directed forward, can easily see objects placed a few yards behind its back; and in many fish, when examined from different points in an aquarium, it is impossible for the observer to place himself in any position, above, behind, or on either side, where he cannot see one or both of the pupils of the animal. The field of vision consequently, for the animal, is a complete sphere; the light being perceptible from every point of the surrounding space. In man, the external borders of the field of vision are very ill defined; and objects placed at a lateral distance of 90 degrees must be very brilliant to attract attention. For practical purposes, the space within which objects are perceptible is one of not more than 75 degrees on each side, or 150 degrees for the entire field of vision.

Line of Direct Vision.—Within the field of vision, however, there is only one point, at its centre, where the form of objects can be perceived with distinctness; and the prolongation of this point, in the visual axis of the eye, from the pupil forward, is called the "line of direct vision." Objects met with upon this line can be distinctly seen; all others, situated upon either side, above or below it, are perceived only in an imperfect manner. If the observer place himself in front of a row of vertical stakes or palisades, he can see those placed directly in front of the eye with perfect distinctness; but those on each side appear as uncertain and confused images. On looking at the middle of a printed page, in the line of direct vision, we see the distinct outlines of the letters; while at successive distances from this point, the eye remaining fixed, we distinguish first only the separate letters with confused outlines, then only the words, and lastly only the lines and spaces.

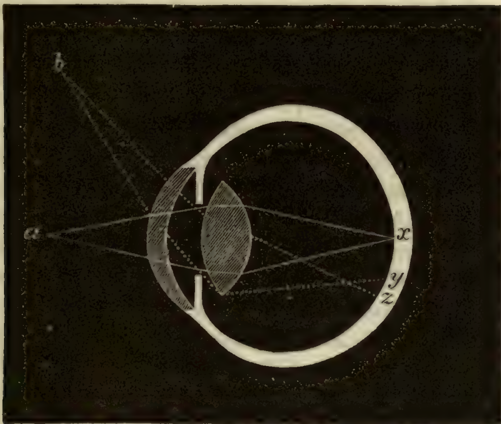
This limitation of serviceable sight to the line of direct vision is practically compensated by the great mobility of the eyeball, which turns successively in different directions; thus shifting the field of vision and examining in turn every part of the space attainable by the eye. In reading a printed page, the eye follows the lines from left to right, seeing each letter and word distinctly in succession. At the end of each line, it returns suddenly to the commencement of the next, repeating the same movement from the top to the bottom of the page.

The deficiency of distinctness outside the line of direct vision depends upon two causes, which are both present, although either separately would tend to produce a similar result; namely, 1st, inaccurate focusing of the luminous rays; and 2d, diminished acuteness of the retinal sensibility.

Rays of light entering the eye from the front, in the line of direct vision, may be brought to an accurate focus at the situation of the retina. But those which enter at a certain degree of obliquity, whether from above, from below, or from one side, suffer a more rapid convergence and are accordingly brought to a focus and again dispersed, before reaching the retina. Thus rays diverging from the point *a* (Fig. 198), in the line of direct vision, are again concentrated at *x*, and form a distinct image upon the retina at that point. But those coming from *b*,

situated considerably on one side, under a similar degree of divergence, fall upon the cornea and the crystalline lens in such a way that there is more difference in their angles of incidence, and consequently more difference in the amount of their refraction. They are therefore brought together too rapidly, and are dispersed upon the retina over the space y, z, forming an imperfect image. Ophthalmoscopic examination of the retina shows that, in point of fact, the images formed at the fundus of

Fig. 198.



Diagrammatic Section of the Eyeball, showing difference of refraction for direct and indirect vision.—*a*, *x*. Rays from a point in the line of direct vision, focussed at the retina. *b*, *y*, *z*. Rays from a point outside the line of direct vision, brought to a focus and dispersed before reaching the retina.

the eye, from luminous objects in the line of direct vision, present perfectly distinct outlines; while those at a certain distance from this point, toward the lateral parts of the retina, are comparatively ill-defined.

Secondly, there is reason to believe that the sensibility of the retina is also less acute in its lateral regions than at the fundus, and particularly at the macula lutea and fovea centralis; since, according to Helmholtz, the sharpness of sight for objects at a little distance from the line of direct vision diminishes in greater proportion than the distinctness of their images formed upon the retina. The fovea centralis, accordingly, is the spot where the retina possesses the most acute sensibility, and it is also situated at the extremity of the visual axis, where the refraction and covergence of the luminous rays are effected with the greatest accuracy. Objects situated upon the line of this axis are seen by *direct* vision, and are distinctly perceived; those situated in the field of view, outside this line, are seen by *indirect* vision, and their outlines appear more or less confused and uncertain.

Point of distinct vision, and Accommodation of the eye for different distances.- An optical instrument, composed of refracting lenses, cannot be made to serve at the same time for near and remote objects. In a refracting telescope or spy-glass, if the instrument be directed toward

any part of the landscape, objects at a certain distance only are distinctly seen; all others, situated within or beyond this distance, are obscure or imperceptible. This is necessarily the case, since a lens or system of lenses can bring to a focus at one spot only those rays which strike its anterior surface within a certain degree of divergence. The formation of a visible image at the desired spot depends entirely upon the refracting power of the lenses being such, that all the rays diverging from a particular point of the object shall be again brought to an exact focus at the plane where the image is to be perceived. If the object be placed at an indefinite distance near the horizon, or if it be one of the heavenly bodies, the rays emanating from any one point of such an object reach the telescope under so slight a degree of divergence that they are nearly parallel; and, on suffering refraction, they will be brought to a focus at a short distance behind the lens. But if the object be less remote, the rays emanating from it strike the lens under a higher degree of divergence. The same amount of refractive power, therefore, produces a less rapid convergence than in the former case, the rays are consequently brought to a focus only at a greater distance behind the lens. To provide for this difficulty, the spy-glass is provided with a sliding tube, by which the distance of the eye-piece from the object-glass may be shifted at will. For the examination of remote objects, the eye-piece is pushed forward, so as to bring into view the image formed at a short distance behind the lens; for the examination of near objects it is drawn backward, to receive the image placed farther to the rear. This is the accommodation of the spy-glass for vision at different distances.

A similar necessity exists in the optical apparatus of the eye. If one eye be covered, and two long needles placed vertically in front of the other, in nearly the same linear range, but at different distances—one, for example, at eight, and the other at twenty inches from the eye—it will be found that they cannot both be seen distinctly at the same time. When we look at the one nearer the eye, so as to perceive its form distinctly, the image of the more remote one becomes confused; and when we see the more distant object in perfection, that which is nearer loses its sharpness of outline.

The same thing may be made evident by stretching in front of the eye, at the distance of seven or eight inches, a plain gauze veil, or other woven fabric formed of fine threads, with tolerably open meshes, so that objects beyond may be readily visible through its tissue. The observer, in using a single eye, may fix at will either the threads of the veil, or the more distant objects placed beyond it; but they alternate with each other in distinctness, like the two needles in the experiment described above. At the time when the threads are sharply defined, other objects are indistinct; and when the eye is fixed upon the more distant objects, so that they are perfectly delineated in the field of vision, the threads of the veil become almost imperceptible, and hardly interfere by their presence with the images seen beyond.

It is evident, therefore, that the eye cannot perceive distinctly, at the same time, objects which are placed at different distances, but it must fix alternately the nearer and the more remote, and examine each in turn. It is also evident that, in thus bringing alternately the one or the other into distinct view, there is a change of some kind in the condition of the eye, by which it adapts itself to the distance or nearness of the object under examination. The observer himself, at the moment of transferring the sight from one object to another, is conscious of a certain effort, by means of which the eye assumes its new condition; and the alteration thus produced is not quite instantaneous, but requires a certain interval for its completion. The process which takes place at this time is the *accommodation of the eye for vision at different distances.*

The method by which the accommodation of the eye is effected forms one of the most important parts of the physiology of sight. The facts which have been established by observation in regard to it are as follows:

I. *The change in ocular accommodation for different distances is accompanied by an alteration in distinctness of the images formed upon the retina.*

This is demonstrated by the observations of Helmholtz with the aid of the ophthalmoscope. When the retina is brought into view by this instrument, if the person under examination fix his attention upon a distant object, its image is shown upon the retina with distinct outlines; but on changing the point of vision for a near object, the image of the latter becomes distinct, while that of the former loses its sharpness. This indicates that the result in question is not produced simply by the mental effort of the individual, but depends upon a physical change in the refractive condition of the eye.

II. *Accommodation for distant objects is a passive condition of the eye; that for near objects is the result of muscular activity.*

This fact is in some degree made apparent by the nature of the sensations accompanying the change. The eye rests without fatigue for an indefinite time upon remote objects; but for the examination of those in close proximity, especially if it be prolonged, a certain effort is necessary, which, after a time, amounts to the sense of fatigue. It is also remarked that solutions of atropine, which, when applied to the eye, cause temporary paralysis of the sphincter muscle of the iris and consequent dilatation of the pupil, suspend, more or less completely, the power of accommodation for near objects, while that for remote objects remains perfect. If both these changes were due to muscular action, it would be necessary to assume that the same substance could paralyze one of the internal muscles of the eyeball, and at the same time leave the other intact, or throw it into a state of permanent rigidity; and there is nothing known which would justify such an assumption. Furthermore, there are certain cases of paralysis of the oculomotorius nerve, where not only the corresponding external muscles of

the eyeball and the sphincter pupillæ are relaxed, but the changes of accommodation are also interfered with; and in these instances, according to Helmholtz, the eye invariably remains adapted for long distances, and cannot be brought to a state of distinct vision for near objects. The evidence in this direction is completed by the well-known facts which accompany the usual diminution or loss of accommodative power with advancing years. In old persons, where this change has taken place, it is the accommodation for near objects which is deficient, while that for distant objects remains perfect.

III. *In accommodation for near objects, the crystalline lens becomes more convex*, thus increasing its refractive power. This is the essential change upon which all the results of accommodation are directly dependent. Its existence was demonstrated by Cramer and Donders,[1] by the aid of what are called the "catoptric images," or images of reflection in the eye. If a brilliant candle flame be so disposed, in a room with dark walls, that its rays fall somewhat obliquely upon the cornea of the eye under observation, and at an angle of about 30 degrees with its line of sight, and if the observer place himself on the opposite side, at an equal angle with the line of sight, three reflected images of the flame will become visible, as in the accompanying figure.

Fig. 199.

CATOPTRIC IMAGES IN THE EYE.—*a.* Upright image of reflection, from the surface of the cornea. *b.* Upright image, from the anterior surface of the lens. *c.* Inverted image, from the posterior surface of the lens.

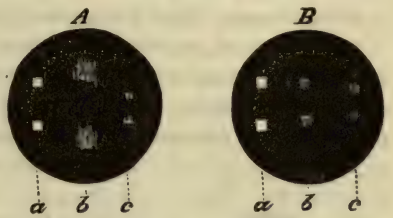
The first left-hand image (Fig. 199, *a*) which is brightest of all, and upright, is that reflected from the surface of the cornea. The second, *b*, which is also upright, but much fainter, is the reflection from the convex anterior surface of the lens; and the third, *c*, which is tolerably distinct, but inverted, is thrown back from the posterior surface of the lens, acting as a concave mirror. If the person under observation now changes his point of sight, from a distant to a near object, the position of the eyeball remaining fixed, the second image, *b*, becomes smaller, and places itself nearer the first. This indicates that the anterior surface of the lens, from which this image is reflected, becomes more bulging, and approaches the cornea; at the same time no change is observable in the other two images, showing that the curvatures, both of the cornea and of the posterior surface of the lens, remain unaltered.

Helmholtz has made the phenomenon above described much more apparent by employing, instead of a single light, two similar sources of illumination placed in the same vertical line. There are thus produced two catoptric images, one above the other, from each surface of reflection; and an increase or diminution in convexity of either of these sur-

[1] DONDERS, Accommodation and Refraction of the Eye, Sydenham edition. London, 1864, p. 10.

faces would be readily manifested by an approach or recession of the two images belonging to it. In accommodation for remote objects (Fig. 200, *A*), the two images from the anterior surface of the lens are of considerable size and somewhat widely separated; in accommodation for near objects (*B*), they diminish in size and approach each other. The double reflections from the cornea and the posterior surface of the lens, remain at sensibly the same distance from each other in both states of accommodation.

Fig. 200.

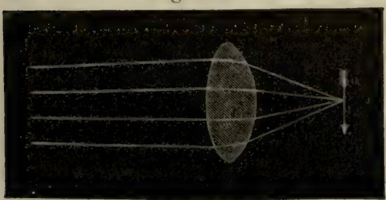


CHANGE OF POSITION IN DOUBLE CATOPTRIC IMAGES during accommodation.—*A*. Position of the images in accommodation for distant objects. *B*. Position of the images in accommodation for near objects. *a*. Corneal image. *b*. Image from anterior surface of lens. *c*. Image from posterior surface of lens.

The advance of the iris and pupil, in consequence of the protrusion of the anterior face of the lens, as remarked by Helmholtz, can also be observed directly, by looking into the eye from the side. If the observer look from this direction so as to obtain a profile view of the cornea and part of the sclerotic between the opening of the eyelids, he will see the dark pupil in perspective under the form of an upright elongated oval, a little in front of the edge of the sclerotic. The person under observation fixes his sight upon a distant object, and the observer places himself steadily in such a position that the hither edge of the iris is just concealed by the anterior border of the sclerotic. If the sight be now shifted from the distant to a near object, in the same linear range, the pupil visibly advances toward the cornea, and the edge of the iris shows itself a little from behind the edge of the sclerotic. If the sight be again directed to the distant object, the pupil recedes and the edge of the iris disappears, as before, behind the sclerotic.

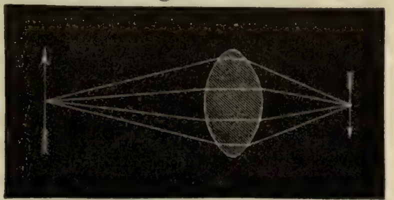
The accommodation of the eye for near objects is therefore produced by an *increased refractive power of the lens*, from the greater bulging

Fig. 201.



VISION FOR DISTANT OBJECTS.

Fig. 202.



VISION FOR NEAR OBJECTS.

of its anterior face. This has the effect of increasing the rapidity of convergence of rays passing through it, and consequently compensates for their greater divergence before entering its substance. In the ordinary condition of ocular repose, when the eye is directed to distant ob-

jects, the rays coming from any point of such an object arrive at the cornea in a nearly parallel position, and are then refracted to such a degree that they meet in a focus at the retina (Fig. 201). When the eye is directed to a nearer point (Fig. 202), the lens increases its anterior convexity; and the divergent rays, being more strongly refracted, are still brought to a focus at the retina, as before. It thus becomes possible to fix alternately, in distinct vision, objects at various distances in front of the eye.

Mechanism of the Change in Figure of the Lens in Accommodation.— The mechanism by which the lens is rendered more convex, in vision for near objects, is far from being completely demonstrated. The reasons have already been given which lead to the conclusion that it is accomplished, in some way, by muscular action; and the two muscles which, separately or together, undoubtedly produce this change, are the *iris* and the *ciliary muscle.*

The iris certainly contracts in accommodation for near objects. This is easily observed on examining by daylight the pupil of an eye which is alternately directed to near and remote objects. The pupil visibly diminishes in size when the eye is fixed upon a point near by, and again enlarges when the sight is accommodated for the distance. The movements of the ciliary muscle, on the other hand, are not subject to observation; but the attachments and position of this muscle have led many writers to attribute to it an important, if not the principal, part in causing a change of form in the crystalline lens.

So far as we are at present able to form a judgment on this question, it may be said that the diminution in size of the pupil is not by itself an efficient cause of accommodation; since, according to Helmholtz, if the observer look through a perforated card, the orifice of which is smaller than the pupil, near objects still appear indistinct when the sight is directed to the distance, and *vice versâ*, notwithstanding the invariable dimensions of the artificial pupil thus employed. The contraction of the circular fibres of the sphincter pupillæ must, therefore, have for its probable object to fix the inner border of the iris, thus affording an internal point of attachment for the radiating fibres of the same muscle. These fibres have for their external attachment the elastic tissue at the inner wall of the canal of Schlemm (Fig. 189); and from this circle also arise the fibres of the ciliary muscle, which radiate outward and backward to their final attachment at the surface of the choroid membrane. If the circular and radiating fibres of both these muscles contract together, they will form a connected system, which may exert a pressure upon the borders of the lens, sufficient to cause the protrusion of its anterior face at the pupil, where alone its advance is not resisted. The aqueous humor, displaced by the protrusion of the lens, may find room in the external parts of the anterior chamber, where the outer border of the iris recedes, under the traction of the ciliary muscle. These are the general features of the mechanical action in accommodation, as it is generally supposed to take place. At the same

time, its details are by no means clearly understood; and explanations, varying more or less from that given above, have been proposed by observers of very high authority. The direction and degree in which pressure would be exerted, by muscular fibres attached like those in the interior of the eye, are too imperfectly known to warrant a positive statement in this respect.

Limits of Accommodation for the Normal Eye.—The normal eye is so constructed that rays emanating from a single point, though coming from an indefinite distance, and therefore sensibly parallel to each other, are brought to a focus at the retina (Fig. 203). Vision is accordingly distinct, even for the heavenly bodies, provided their light be neither too dim nor too excessive in brilliancy. For bodies situated nearer to the eye, the convexity of the lens increases with the diminution of the distance, and vision still remains perfect. But there is a limit to the change of shape which the lens is capable of assuming; and when this limit is reached, a closer approximation of the object necessarily destroys the accuracy of its image. For ordinary normal eyes, in the early or middle periods of life, accommodation fails and vision becomes indistinct, when the object is placed at less than 15 centimetres (6 inches) from the eye.

Between these two limits, of 15 centimetres and infinity, the amount of accommodation required is by no means in simple proportion to the variation of the distance. The change of accommodation necessary for objects situated respectively at 15 and 30 centimetres from the eye (6 inches and 12 inches), is much greater than that corresponding to the distances of one yard and two yards. The farther the object recedes from the eye, the less difference is produced, in the sensible divergence of the rays, by any additional increase of distance; and consequently less variation is required in the refractive condition of the eye to preserve the accuracy of its image. It is generally found that no sensible effort of accommodation is required for objects situated at any distance beyond fifty feet from the observer; while within this limit the amount of accommodation necessary for distinct vision increases rapidly with the diminution of the distance.

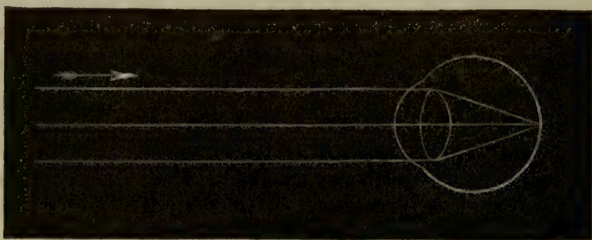
An eye which is capable of accommodating for distinct vision, throughout the whole range included between 15 centimetres and an indefinite distance, is, in this respect, a normal eye, and is said to be *emmetropic;* that is, its powers of accommodation are placed within the natural limits or measurements of this function.

Presbyopic Eye.—The power of accommodation diminishes naturally with the advance of age; and observation shows that this diminution dates from the earliest period of life. Infants often examine minute objects at very short distances, in a manner which would be quite impracticable for the healthy adult eye; and the minimum distance of distinct vision at twenty years of age is placed by some writers at ten centimetres instead of fifteen. The power of increasing the convexity of the lens to this extent is soon lost; and, as it continues to diminish, a time arrives, usually between the ages of 40 and 50 years, when the incapacity

of accommodation for near objects begins to interfere with the ordinary occupations of life. When this condition is established the eye is said to be *presbyopic.* Its vision is still perfect for distant objects, but it can no longer adapt itself for the examination of those in close proximity to the eye. To remedy this defect the patient employs a convex eye-glass, which replaces for him the increased convexity of the crystalline lens, in accommodation for near objects; and by the aid of such a glass he is able to read or write at ordinary distances and in characters of the ordinary size.

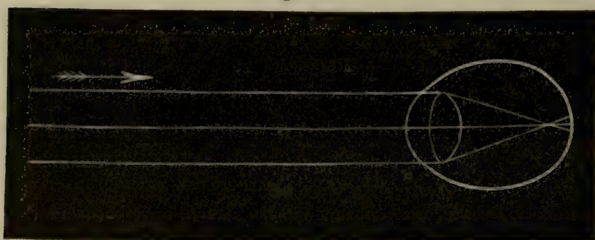
The use of a convex eye-glass does not restore the perfection of sight as it existed beforehand. In the normal eye, the degree of accommodation varies for every change of distance within fifty feet; and the organ is thus adjusted, by an instantaneous and unconscious movement, for the most delicate variations of refractive power. But an eye-glass, the curvatures of which are invariable, can give perfect correction only for a single distance. A glass is, therefore, usually selected of such a strength as to serve for the most convenient distance in the ordinary manipulation of near objects.

Fig. 203.



Emmetropic Eye, in vision at long distances. (Wundt.)

Fig. 204.



Myopic Eye, in vision at long distances. (Wundt.)

Myopic Eye.—In many instances, where the eye is otherwise of normal configuration, its antero-posterior diameter is longer than usual, thus placing the retina at a greater distance behind the lens. The consequence of this peculiarity is that while the luminous rays are brought to a focus at the usual distance from their point of entrance into the eye, this focus is situated within the vitreous body; and the rays reach the retina only after they have crossed and suffered a partial dispersion.

(Fig. 204.) This produces an indistinct image for all remote objects. Within, however, a certain distance from the eye, the rays enter the pupil under such a degree of divergence, that their focus behind the lens falls at the situation of the retina, and the object is distinctly seen. Such an eye is said to be *myopic*, or, in ordinary language, "near sighted," because its range of distinct vision is confined to objects situated comparatively near the eye. The flexibility of the lens, and its capacity for increasing its convexity, may be, in the myopic eye, fully up to the normal standard, and consequently its power of accommodation may be as great in reality, though not in distance, as that of the normal eye. In the emmetropic condition, a certain degree of variation in the curvature of the lens produces the necessary change of accommodation for any distance between 15 centimetres and infinity. In the myopic eye the same amount of accommodating power may be present, though perfectly distinct vision be confined between the distances of 8 and 20 centimetres. The myopic eye consequently has distinct vision at shorter distances than a natural one, but gives an imperfect image for remote objects.

The remedy adopted for the myopic eye is to employ a concave eye-glass, which increases the divergence of the incident rays. This enables the eye to bring parallel or nearly parallel rays to a focus situated farther back than it would otherwise fall, and at the actual position of the retina; thus giving distinct vision for remote objects. As the accommodative power is normal in amount, this contrivance restores completely the perfection of sight, in a myopic eye which is otherwise well-formed; and the patient can then accommodate accurately for all distances within the natural limits of distinct vision.

Apparent Position of Objects, and Binocular Vision.—The apparent position of an object is determined by the direction in which the luminous rays pass from it to the interior of the eye. The perception of the light itself necessarily marks the direction from which it has arrived, and therefore the apparent position of its source. It is difficult to understand fully the precise physiological conditions which cause this appreciation of the path followed by a luminous beam; although there seems reason for the belief that it is in some way connected with the position of the rods and cones which stand perpendicularly to the curved surface of the retina, and thus receive the impression of a ray, if at all, in the direction of their longitudinal axes. But whatever may be the optical or physiological mechanism of the process, its plain result is that a ray coming from below attracts attention to the inferior part of the field of vision; and one coming from above is referred to its point of origin in the upper part of the same field. Thus if two luminous points appear simultaneously in the field of vision, they present themselves in a certain position with regard to each other, above or below, to the right or the left, according to the direction in which their light has reached the eye.

This fact is fully demonstrated by the phenomena of angular reflection and refraction. If a candle be held behind the back, in such a position as to be reflected in a mirror placed at the front, the light presents itself to the eye as if it were really in front, because it is from this direction that the luminous rays finally come. If we observe the reflection of objects in a mirror held horizontally, or in a smooth sheet of water, the objects seem to be placed below the reflecting surface, although they are really above it; since the rays which make their impression upon the eye actually come from below. A stick or pebble, seen obliquely at the bottom of a transparent pool, appears nearer the surface than it really is, because the rays which reach the visual organ have been bent from their course, in passing from the water into the atmosphere, and have consequently assumed a more oblique direction.

Erect Vision, with Inverted Retinal Image.—Since it is the direction of the visual rays, rather than the point of their impact upon the retina, which determines the apparent relative position of luminous objects, such objects appear erect although their images upon the retina are inverted. The retinal image is not the form which is seen by the eye itself, but is only a phenomenon visible to the inspection of another eye. It is an appearance which is incidental to the mode of refraction of the visual rays; and its position is quite a distinct matter from that of the luminous impressions perceived by the retina. Its relation to the picture really presented to the sensitive membrane, is like that of the reversed engraving upon a wood-cut to the printed impression of the same design; or like that of the elevations and depressions of a mould to the depressions and elevations of the cast taken from it. In the field of sight, therefore, for each eye, every object appears above or below, to the right or left, according to the position which it really occupies in regard to the centre of the field and the line of direct vision.

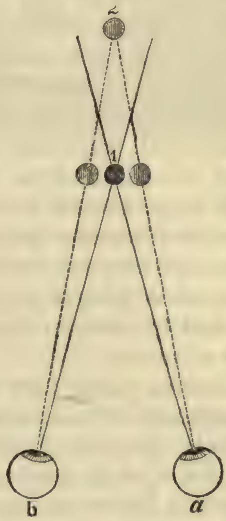
Point of Fixation, in Vision with Two Eyes.—For each eye, distinct perception is possible, as shown above (p. 628), only for objects situated in a single range, which is known as the "line of direct vision." Since the eyes are placed in their orbits at a lateral distance from each other of about six centimetres, when they are both directed at the same object, within a moderate distance, their lines of direct vision have a sensible convergence, and, of course, cross each other only at a single point. At this point of intersection of the two lines of direct vision, an object may be seen distinctly by both eyes at the same time. But at every other point, it must appear indistinct to one of them; because if it be in the line of direct vision for the right eye it will be out of that line for the left, and *vice versâ.* There is, accordingly, only a certain distance, directly in front, at which an object can be distinctly seen simultaneously by both eyes; namely, that at which the two lines of direct vision cross each other. This point is called the *point of fixation*, for the two eyes. In fixing any object, for binocular vision, the accommodation in each eye is at the same time adjusted for the required distance;

and thus the entire accuracy of both organs is concentrated upon a single point.

Since it is the position of the two eyes in their respective orbits which determines the point of fixation, the observer can form a tolerably accurate judgment, as to whether another person within a moderate distance be looking at him, or at some other object farther removed in the same direction. For more considerable distances the estimate fails, because the obliquity of the two eyes, which varies perceptibly within moderate distances, diminishes so much in looking at remote objects, that the slight differences which exist are no longer appreciable by the observer.

Single and Distinct Vision with both Eyes.—From the preceding facts it is evident that only one point can be found in the line of direct vision, for both eyes at the same time. When an object occupies this situation, namely, the point of fixation, it is distinctly perceived by both eyes in the centre of the field of vision; thus its two visual images exactly cover each other in their apparent position and so form but one. Consequently, the object appears single, though seen simultaneously by both eyes (Fig. 205). But if placed either within or beyond the point of fixation, an object appears indistinct and at the same time double. If the observer hold a slender rod in the vertical position at a distance of one or two feet before the face, and in the same range with any small object, such as a door-knob, on the opposite side of the room, it will be found that when both eyes are directed at the rod, it is seen single and distinctly, but the door-knob appears double one of its images falling upon each side. If the eyes be now directed at the door-knob, that in turn becomes distinct and single, while the rod appears double, one indistinct image being placed on each side, as before.

Fig. 205.



Single and Double Vision, at different distances.—*a.* Right eye. *b.* Left eye. 1. Object at the point of fixation, seen single. 2. Object beyond the point of fixation, seen double.

These phenomena depend upon the different directions of the two lines of direct vision. When the eyes are so directed that the nearer object (Fig. 205, 1) occupies the point of fixation, the farther object (2) will also be seen, because it is still included in the visual field; although it will be seen indistinctly, because the accommodation of the eye is no longer adjusted to its distance, and because it is not in the line of direct vision. But for the right eye (*a*) it will be placed to the right of this line, and for the left eye (*b*) to the left of it. Its two images do not correspond with each other in situation, and the object accordingly appears double.

If the eyes, on the other hand, be directed at the more distant object,

the nearer one is no longer in the point of fixation. For the right eye, its image will appear to the left of the line of direct vision, and for the left eye to the right of this line. It therefore appears double and indistinct.

Thus, in the ordinary use of binocular vision every object but one appears double and at the same time imperfectly delineated. This circumstance is so little noticed that it is never a source of confusion for the sight, and even requires a special experiment to demonstrate its existence. The reason for its passing, as a general rule, unobserved is twofold. First, the attention is naturally concentrated upon the object which is placed, for the moment, at the point of fixation. When this point is shifted, the new object upon which it falls also appears single; and thus the idea of a double image, even if indistinctly suggested at any time, is at once dispelled by the movement of the eyes in that direction. Secondly, an object which is really placed in any degree toward the right hand or the left will form an indistinct double image, since it occupies a different apparent position for the two eyes. But the obliquity of its rays, and consequently the indistinctness of its image, will be greater for the right eye than for the left, or *vice versâ;* and the notice of the observer, if drawn to it at all, is occupied with the more distinct of the two images, to the exclusion of the other. The fact becomes palpable only in such an experiment as that detailed above; where two bodies are examined in the same linear range, so that the double images produced are equal in intensity, and sufficiently detached by contrast from surrounding objects to force themselves upon the attention.

Double vision may also be produced at any time by pressure with the finger at the external angle of one of the eyes, so as to alter its position in the orbit, the other eye remaining untouched. But in this case it is the whole field of vision which is displaced, and all objects are doubled indiscriminately; their images being separated to the same degree and in the same direction, whatever may be their distance from the eye. It is this form of double vision which is produced, in vertigo or intoxication, by irregular action of the muscles of the eyeball.

Appreciation of Solidity and Projection.—When both eyes are directed simultaneously at a single point, the distance of the object may be estimated with considerable accuracy by the degree of convergence of the visual axes required for its fixation. Since this convergence is in proportion to the proximity to the observer of the point of fixation, another impression, of different kind but of equal importance, is also produced by binocular vision, when the object has an appreciable volume and thickness, and when it is placed within a moderate distance. Owing to the lateral separation of the two eyes, and the convergent direction of their visual axes, they do not both receive from such an object precisely the same image. Both eyes will see the front of the object in nearly the same manner; but in addition the right eye will see a little of its right side, and the left eye will see a little of its left side. This

is illustrated in Figs. 206 and 207, which represent a skull as seen by the two eyes, when placed exactly in front of the observor at a distance of eighteen inches or two feet; rather more of the details on one side being visible to the left eye, and rather more of those on the other

Fig. 206.

As seen by the Left Eye.

Fig. 207.

As seen by the Right Eye.

being visible to the right eye. As the central part of the mass is in the point of fixation, at the junction of the two visual axes, the object appears single. But the images which it presents to the two eyes are not precisely identical in form; and it is the combination of these different images into one which gives rise to the impression of *solidity* or *projection.*

But this effect is complete only when the object is situated within a moderately short distance. For those which are comparatively remote, the convergence of the visual axes, and consequently the difference in the apparent configuration of the two images, become inappreciable, and the optical impression of solidity disappears. At a distance of some miles even a large object, like a mountain, loses its projection, and presents the form of a flattened mass against the horizon. It is on this account that pictorial representations of distant views are often extremely effective; the idea of successive remoteness in different parts of the landscape being conveyed by appropriate intersection of the outlines and by variations in tone, color, and distinctness, like those due to the interposition of the atmosphere. On the other hand, a picture of near objects, which aims to represent their solidity, can never deceive us in this respect, however elaborate may be the details of surface, shadow, and color; since the flat surface of the picture presents the same image to both eyes, and it is consequently evident that the objects delineated have no real projection. But if two pictures of the same object, taken in two different positions, be presented in such a way that only one of them is seen by the right eye, and only the other by the left, the same optical effect may be produced as by the object itself, and the appearance of solidity and projection may be perfectly

imitated. Such is the principle of the instrument known as the *stereoscope*. This is simply a box or framework, holding two photographic pictures of the same object, which have been taken from two different points of view, corresponding to the different positions of the two eyes. Thus one of the pictures represents the object as it would in reality be seen by the right eye, and the other represents it as it would be seen by the left. When these pictures are so placed in the stereoscope that each eye has presented to it the appropriate view, the two images, occupying the point of fixation, are fused upon the retina, and produce an extremely deceptive resemblance to the projection and stolidity of the real object.

The acuteness of perception, by which the eyes appreciate a slight difference in the two retinal images, is the measure of what may be called their *stereoscopic sensibility.* It has been observed that two coins, composed of different metals, but struck from the same die, are slightly different in volume, owing to the unequal dilatation of the metals after receiving the impression of the die. This difference may be quite inappreciable to the eye in ordinary examination, even when the coins are placed in contact with each other; but if they be made to take the place of the two pictures in a stereoscope box and viewed together, the resulting image, instead of presenting a plane surface, appears oblique and convex.

The degree of stereoscopic sensibility was tested by Helmholtz in the following manner: Three metallic pins were fixed upright in small movable blocks of wood, placed side by side, so that the pins should be about 12 millimetres distant from each other, and nearly in the same vertical plane. The observer then, using both eyes simultaneously, examined the appearance of the objects from a distance of 340 millimetres, the pins being arranged at right angles across the line of view. The immediate object of the examination was to determine, from the stereoscopic effect, whether the three pins were placed exactly in the same plane, or whether either of them were in advance of or behind the others. It was found possible to detect in this way a deviation in position of one of the pins equal to one-half its own thickness, that is, 0.25 mm.; and the deviation was recognized with absolute certainty when it amounted to the entire thickness of the pin, that is, 0.50 millimetre.

General Laws of Visual Perception.—Beside the laws regulating the formation and combination of optical images, there are certain phenomena connected with visual perceptions in general, which are of considerable importance in the physiology of sight. Some of these phenomena require for their study special modes of investigation, while others are made evident by comparatively simple means, and are often of consequence in their hygienic relations.

Luminous impressions upon the eye remain for a certain time after the cessation of the light. The persistence of luminous impressions thus left upon the eye is very short, and is not usually noticeable,

because these impressions are, under all ordinary conditions, immediately followed by others upon the same part of the retina, and the new sensation practically obliterates the old one. But, if the instantaneous impression be not followed by a different one, or if it be sufficiently vivid to be perceived, notwithstanding the presence of others, its continuance may be made evident to observation. Thus, in a dark room, if a bright point, like the heated end of a wire, be carried round in a circle with moderate rapidity, the eye follows its movement, as it presents itself successively in different parts of the circle; the light always appearing at one point only, the rest of the space remaining dark. But if the rapidity of the circular movement be greatly increased, the bright point seems to be drawn out more or less into a curved line; and, when the rate of revolution has attained a very high degree of velocity, it becomes transformed into a continuous circle of light, since the impression made upon the retina, when the end of the wire is at one part of the circle, lasts until it has completed a revolution and again returned to the same point. The succession of sparks thrown off rapidly from a knife-grinder's wheel often produce the effect, even by daylight, of an unbroken stream of fire. A circular saw with large teeth, driven by machinery under a high rate of speed, presents apparently a perfectly smooth edge, the outline of which is formed by the moving points of the teeth; and the revolving spokes of a carriage wheel, in rapid motion, become confused upon the retina with each other and with the intervening spaces, and assume the appearance of a uniform glimmering disk.

The absolute duration of visual impressions upon the retina has been the subject of various researches, but it is found that its length cannot be expressed by any single number which would be correct for all cases. A brilliant light leaves, on the whole, an impression which lasts longer than that from a feeble one; but, on the other hand, its relative intensity to the light of surrounding objects diminishes more rapidly, and consequently, when it is in motion, a higher degree of velocity is required to produce the appearance of a uniformly bright line. The experiments employed to determine the length of time, during which a luminous impression remains upon the eye without appreciable diminution of its intensity, have been usually those with revolving disks, the surface of which is variegated in sectors of black and white. The rate of revolution of the disk being known, as well as the width of the different sectors, when the revolving surface presents to the eye the appearance of an absolutely uniform gray tint, the time during which the black or white impressions remain undiminished in strength is readily ascertained. The result obtained, from experiments conducted in this manner, under moderate illumination, gives the duration of perfect visual impressions as one twenty-fourth of a second, and, for the oscillation of a very luminous point following the vibrations of a tuning fork, one-thirtieth of a second.

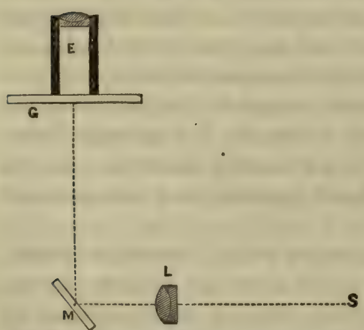
The persistence and apparent continuity of successive visual images, appearing at the same spot, is illustrated in the optical contrivance known as the *Thaumatrope*, or magic wheel. It consists of an opaque

disk, with a perforation at one spot near its edge, through which another disk is visible, placed immediately behind the first, and capable of revolving rapidly while the first remains stationary. Upon the second disk is a circle of pictures representing the same figure in different positions; and when, by its revolution, these pictures are made to pass in quick succession across the opening of the disk in front, they present the appearance of a single figure in rapid motion. The interval between the perception by the eye of successive pictures is too short to be observed, and the same object appears to take successively the different positions in which it is represented.

Duration of a Luminous Impulse required for the Perception of Visual Impressions.—This point has been investigated by Rood[1] by means of the light of an electric spark obtained from an induction coil connected by its terminal wires with the inner and outer surfaces of a Leyden jar. On breaking the primary current a discharge takes place between the electrodes, which is of exceedingly short duration. This duration was measured by Prof. Rood with the aid of a mirror revolving upon its transverse axis, by which the light of the electric spark was thrown upon a plate of glass, where it could be examined by the naked eye, or with a magnifying eye-piece, as in Fig. 208.

The light emanating from the spark S, was received by an achromatic lens L, of nine inches focal length. It then fell upon a plane mirror revolving with a uniform velocity of 340 times per second, and, after reflection by the mirror, was brought to a focus upon a glass plate G, where it could be examined by the telescope eye-piece E, magnifying ten diameters. From the known rate of revolution of the mirror, and its distance from the glass plate G, the necessary rate of movement of a reflected beam upon the plate was determined. If the spark, used in these experiments, lasted long enough for its reflected image to move over an appreciable distance, this image would appear to the eye to be drawn out in the direction of the movement, owing to the persistence of its visual impression as described above. But with the mirror revolving at this speed no such deformation was perceptible, the spark image appearing of precisely the same form as if the mirror were stationary; showing that the duration of the light could not be greater than .000002 ($\frac{1}{500,000}$) of a second.

Fig. 208.



APPARATUS for measuring the duration of an electric spark.—S. Position of the spark. L. Achromatic lens. M. Revolving mirror. G. Glass plate for receiving the image of the spark. E. Telescope eye-piece.

[1] The American Journal of Science and Arts. New Haven, September, 1871.

In a continuation of the experiments, there was interposed between the spark and the mirror a blackened glass plate, ruled with parallel transparent lines $\frac{1}{24}$ of a millimetre in width, and separated from each other by the same distance. The image of this plate, when illuminated by the spark, would appear upon the glass G, so long as the mirror were stationary, as a series of equal alternating black and white lines. With the mirror in motion, if the illumination lasted long enough for the image to be shifted a distance equal to the combined width of a black and white line, these lines would become undistinguishable from each other, as in the case of the revolving disk with black and white sectors. Thus the continuance of the visible lines, under a given rate of motion, proved that the duration of the electric spark was less than a certain calculable period. Their disappearance as distinct objects indicated that the limits of this duration had been reached; and that it was long enough to allow of the shifting of two adjacent lines. The result showed that the duration of the shortest measurable spark was but little over .00000004 ($\frac{1}{25,000,000}$) of a second.

With a spark of this duration, distinct vision of motionless objects was perfectly possible. The letters on a printed page were plainly to be seen, and even the phenomena of polarization of light distinctly observable. It is accordingly sufficient to produce a complete retinal impression.

These experiments do not indicate the time required for the necessary nervous action in the perception of light. They only show that a luminous impulse having the above duration is sufficient to cause a distinct sensation. But the time which is requisite for the sensation to be perceived is very much longer. From the results given in a preceding chapter (p. 431) it appears that the transmission of a luminous impression through the optic nerve, would undoubtedly require at least $\frac{1}{1000}$ of a second, and its perception in the brain considerably more. It follows from this that, at the instant when the image of the electric spark is seen, in the experiment of Prof. Rood, it has, in fact, already disappeared; the interval which elapses between its actual occurrence and its perception by the observer being very much greater than the duration of the spark itself.

The facts detailed above explain the cause of a peculiar optical effect, which has often been observed under the use of the electric spark; namely, that bodies in rapid motion, if illuminated by an instantaneous discharge, appear to the observer as if at rest. A disk, painted with black and white sectors, if set in revolution under continuous light, appears of a uniform gray; or, if the sectors be painted of the rainbow colors, their tints are mingled and the disk appears white. But if such a disk, revolving in a dark room, be illuminated by the electric spark, it becomes visible for an instant, with its different sectors as distinct from each other as if they were at rest. A jet of water discharged from an orifice at the bottom of a vessel, though transparent in the immediate neighborhood of the orifice, is turbid lower down; and by instan-

taneous illumination the turbid portion is seen to be composed of separate drops, which appear to be motionless. A flash of lightning has a similar effect in exhibiting objects which are in motion as if they were quiescent. The passage of a cannon ball or a rifle bullet by daylight is imperceptible; because, as an opaque object, it does not remain long enough at any one point to efface the persistent impression of the objects visible behind it, and the sight of these objects accordingly does not appear to have suffered any interruption. But if such a missile should happen to be passing in front of the observer in the night time during a thunder storm, at the moment of a flash, it would be visible equally with the other parts of the landscape, and would appear as a motionless object suspended in the air.

The momentary closure of the eyes in winking, for the same reason, does not cause any noticeable interference with sight, and is not even observed by the individual; since the visual impression of external objects appears to be continuous during the short interval occupied by the movement of the lids.

The local sensibility of the retina is diminished by continued visual impressions. This diminution of the retinal sensibility appears to be continuous from the very commencement of a visual impression, so that it may be made perceptible within a few seconds. In the experiment of exhibiting the image of the retinal bloodvessels by changing the position of their shadows (page 622) these shadows are visible for an instant with extreme sharpness. But they begin to fade almost at once and after a short interval become imperceptible. They can only be seen for a considerable time, by keeping the light in motion, so that the shadows fall alternately upon different parts of the retina. The portions of the retina which are in full illumination have their sensibility so rapidly diminished, that the shadow, if motionless, is no longer visible by contrast. Those which are in shadow, on the other hand, become comparatively more sensitive by repose; and when the shifting of the light brings them again into illumination, they not only receive more stimulus than the adjacent parts, but are also more impressible to its influence.

If one eye be covered by a dark glass, and the other be used exclusively, for an hour or two, in reading or writing, at the end of that time the difference in retinal sensibility of the two eyes will be very apparent. A single faintly luminous object in a dark room may then be almost imperceptible to the eye which has been in use, while it will appear to the other quite brilliant. If the application of the eye have not been carried beyond the bounds of moderation, this difference is transitory; and by reversing the conditions, that is, covering the eye previously in use, and reading or writing by aid of the other, that which was before the most sensitive to light becomes less so, and that which was previously fatigued recovers its sensibility.

The alternate diminution and recovery of the retinal sensibility, by excitement and repose, is directly connected with the phenomena of *negative images.* If the eye be steadily fixed for a short time upon a

white spot in the middle of a black ground, and then suddenly directed toward a blank wall of a uniform white or light gray color, a dark spot will appear at its centre, of the same apparent size and figure with the white one previously observed. This is the "negative image" of the retinal impression. That part of the retina which was first impressed by the rays from the white spot becomes less sensitive to light; and another white surface, looked at immediately afterward, appears darker than usual. On the other hand, those parts which were exposed only to the dark ground, that is, to the comparative absence of light, are more sensitive than before; and the surface of the white wall, outside the central spot, appears brighter than usual. It is not necessary that the contrast in hue between the different parts of a retinal image should be as strong as that of black and white, in order to produce this effect. Any decided difference in illumination will be sufficient. It is not even essential to look at a different background, to observe the appearance in question. If a piece of furniture of dark wood be placed against a blank wall of white or gray surface, and looked at steadily for a short time, on shifting the eyes to a different part of the same wall, the figure of the chair or table will appear, with all its details of outline, expressed in a lighter tint than that of the surrounding parts.

The above effect may be also produced in a still more simple manner. Let a black ruler, about one inch wide, be laid upon a sheet of white paper, and looked at steadily for thirty or forty seconds. If the ruler be now removed by a sudden motion, the eye remaining fixed, its image will appear as a bright band upon the paper, fading gradually as the sensibility of the retina becomes equalized in its different parts.

If the figure which is thus examined be a colored one, its negative image, subsequently produced, will present a complementary hue to that of the original object. A strip of red paper placed upon the white sheet, and then suddenly removed, leaves a negative image which is bluish-green; and a green one leaves an image which has a decided tinge of red. This shows that the sensibility of the retina may be increased or diminished separately for the different colored rays of the luminous beam. While looking at a red object, the retina becomes less sensitive to the red rays, but more so for those at the opposite end of the spectrum, and *vice versâ;* so that, on looking subsequently at a white object, the negative image exhibits a tint corresponding to the rays for which the retina has remained most sensitive. That this is the mechanism of the production of complementary colors in negative images becomes evident on simplifying the experiment. If the black ruler be laid upon a book bound in blue cloth, on taking it away the band which remains in its place is of a more intense blue than the rest. If a red book be used for the same purpose, the negative image of the ruler presents a remarkably pure red color, while the remainder of the surface appears of a dull brown.

The variable sensibility of the retina, according to its exposure, affords an explanation of the well-known fact, that under some condi-

tions an object may be most easily perceived by indirect vision. It often happens that in searching for a star of very small magnitude and feeble light, it may be momentarily perceived by looking not directly at it, but at a point in its immediate neighborhood, at a small angular distance from its real position. The star is not seen distinctly under these circumstances, because it is out of the line of direct vision. But its light falls upon a part of the retina near the fovea centralis, the sensibility of which is more acute than usual, owing to its continued exposure only to the dark sky; while the fovea itself, which has been receiving in succession the images of particular stars, is comparatively deficient in impressibility to light. When the visual axis is turned directly upon the fainter star, for the purpose of getting a distinct image, its light disappears; and thus it can only be seen as an evanescent object by indirect vision.

If the eye be fixed immovably for too long a time upon the same luminous object, the local diminution of retinal sensibility may amount to fatigue; and a persistence in its continuous application may produce permanent injury of the visual organ. After steadily examining a single object for even a short time, it becomes difficult to resist the tendency to turn the sight in another direction by the automatic movement of the muscles of the eyeball. Naturally, the eye never rests for more than a few seconds upon any one point in the field of view; but is directed in succession at different objects, fixing each one in turn at the point of distinct vision, and immediately passing to another more or less remote. Thus the fatigue of the retina is avoided, since those parts which at one instant have a stronger illumination, at the next receive the impression of a shadow; and no portion of the membrane is exposed sufficiently long to any single object to become insensible to its grade of light or color.

There is also reason to believe that the eye requires, for its safety, the periodical suspension of all visual impressions which is obtainable in *sleep*. It is not essentially different in this respect from other parts of the nervous apparatus of animal life; but the delicacy of its sensibility, which is requisite for the due performance of its function, and the complication of its structure, which includes so many parts adjusted to each other with mathematical accuracy, indicate that it is one of the organs most liable to derangement if deprived of its natural interval of restoration and repose.

Sense of Hearing.

By the sense of hearing we receive the impressions of sound, and appreciate their intensity, their tone or pitch, with all the variations of higher or lower notes, as well as their quality, that is, the different character of sounds of the same tone and intensity, but produced by different methods, as by reeds, strings, or wind instruments, or by the concussion of solid bodies. Our idea of *time*, or the succession of events, seems also to be connected more especially with auditory sensa-

tions. The impressions received in this way depend upon the vibrations excited in the atmosphere by sonorous bodies, which are themselves thrown into vibration by various causes, and which then communicate similar undulations to the surrounding air. These undulations are of such a kind that they cannot be directly appreciated by the organs of general sensibility; but when communicated to the auditory apparatus they produce, through it, the sensation of sound.

Organ of Hearing.—The organ of hearing consist of, first, the *external ear*, a conch or trumpet-shaped expansion, destined to collect the sonorous impulses coming from various quarters, and to conduct them into its tubular continuation, the external auditory meatus; secondly, a membranous sheet or drum-head, the *membrana tympani*, stretched across the bottom of the external auditory meatus, by which the sonorous vibrations are received and transmitted, through the chain of bones or auditory ossicles, across the cavity of the tympanum or middle ear, to the third portion of the auditory apparatus, namely, the *labyrinth*, or internal ear; a cavity excavated in the petrous portion of the temporal bone, filled with fluid, and containing various membranous sacs and canals, upon which are distributed the filaments of the auditory nerve.

Thus the delicate terminal expansions of the auditory nerve, deeply concealed in their bony cavities, and sustained by the surrounding fluid, are protected from all other mechanical impressions, but are so placed as to receive the impulse of sonorous vibrations.

External Ear.—The external ear consists of a cartilaginous framework, covered with integument, loosely attached to the bones of the head, and more or less movable by means of various muscles, which, by their contractions, tend to turn its concavity in various directions. In man, notwithstanding the existence of these muscles, their functional activity is nearly imperceptible; and it is only in exceptional cases that they are capable of producing a partial sliding or rotatory movement of the external ear. In most of the quadrupeds, on the other hand, these movements are vigorous and extensive, and play an important part, not only in the changes of expression by varying the attitude of the external ear, but also in aid of the sense of hearing, by enabling the animal to catch distinctly the sonorous vibrations, from whatever quarter they may come. By their assistance the direction of a sound is also appreciated, since the animal ascertains, in placing the ear in different positions, the region from which it is received with the greatest distinctness.

Membrana Tympani and the Chain of Bones.—The membrana tympani is a fibrous sheet of circular form, composed of a principal layer not more than 0.05 millimetre in thickness, but quite strong, and consisting of circular and radiating tendinous fibres with a trace of intermingled elastic fibres. Its external and internal surfaces respectively are covered by thin continuations of the integument of the external auditory meatus on the one hand, and of the mucous membrane of the

tympanic cavity on the other; and all three layers together form a membrane which is about 0.10 millimetre thick.

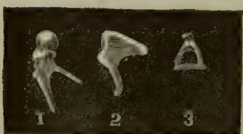
In its natural condition the membrane is drawn inward, by its attachment to the handle of the malleus, in such a way that its external surface exhibits a funnel-shaped depression, the deepest point or bottom of which corresponds to the situation of the end of the handle of the malleus. According to the observations of Helmholtz,[1] the sides of this funnel-shaped depression are not plane but convex, somewhat like the inner surface of the blossom of a morning-glory. It is only along a single line, corresponding to the attachment of the handle of the malleus, that the meridian of the funnel would be a nearly straight line; elsewhere the radial fibres of the membrana tympani are curved, with their convexities looking toward the external auditory meatus.

As the only attachment of the membrana tympani, except at its circular border where it adheres to the bony walls of the meatus, is to the movable handle of the malleus, any movement of the handle of the malleus inward will draw the membrana tympani in the same direction, deepen the funnel-shaped depression at its centre, and put its fibres more upon the stretch. On the other hand, a movement of the membrana tympani outward will draw the handle of the malleus outward; and, finally, if the malleus be held in a position of equilibrium, by its elastic and muscular attachments internally to the membrana tympani, any movement of this membrane, either outward or inward, will be followed by a corresponding change of position in the malleus itself.

This is the physiological action of the membrana tympani. From its thinness and tension and from its position at the bottom of the external auditory meatus, it enters into vibration, under the impulse of sound coming from the exterior, and communicates similar movements to the handle of the malleus attached to its internal surface.

The chain of bones consists of three ossicles, articulated with each other by their corresponding extremities, and forming a zigzag line of jointed levers, extending from without inward, across the cavity of the tympanum. They are known respectively, from the resemblances of their configuration, as the "malleus," "incus," and "stapes," or the hammer, the anvil, and the stirrup. The malleus is about nine millimetres in length, of which a little more than one-third is occupied by the rounded head and the neck, and a little less than two-thirds by the comparatively straight and tapering handle. The very slender long process projects laterally in a nearly horizontal direction from behind forward in the natural position of the bone. The handle is the only part of the malleus which is adherent to the membrana

Fig. 209.



OSSICLES of the human ear.—1. Malleus. 2. Incus. 3. Stapes. (Rüdinger.)

[1] Mechanism of the Ossicles of the Ear. Translated by Albert H. Buck, M.D., and Normand Smith, M.D. New York, 1873, p. 20.

tympani, the neck corresponding to the upper border of this membrane, while the head projects above it, lying comparatively free in the cavity of the tympanum. It is, however, maintained more or less closely in its position by thin ligamentous bands arising from the bony wall of the tympanic cavity and inserted into its head and neck, and by the tendon of the internal muscle of the malleus or "tensor tympani," which, coming from a direction anterior and internal to the bone, is inserted into the upper extremity of its handle. The action of this muscle is to draw the handle of the malleus inward, tightening the membrana tympani, and rotating the head of the malleus slightly outward. The principal movement of the malleus is therefore a rocking, to and fro movement, about a nearly horizontal axis situated at the junction of the handle and the neck.

The head of the malleus is articulated with the body of the incus by a capsular joint with double-inclined surfaces. As Helmholtz has shown, the surfaces are so different in their inclination, one being very steep, the other but slightly oblique, that when the handle of the malleus is drawn inward, the two articular surfaces lock together, and the incus follows the movement of the malleus; but when the latter bone is drawn outward, the surfaces may glide upon each other, without the incus necessarily moving at the same time.

The third bone of the middle ear, the stapes, has in its form the most exact resemblance to its namesake, an ordinary metallic stirrup. It is articulated by its angular extremity to the lower end of the long arm of the incus in such a manner as to be nearly horizontal in position, its

Fig. 210.

RIGHT TEMPORAL BONE of the new-born infant, seen from its inner side; showing the internal surface of the membrana tympani and the chain of bones in their natural position. (Rüdinger.)

two arms being placed, one anteriorly the other posteriorly. Its oval base corresponds in form, and nearly in size, with the fenestra ovalis of the bony labyrinth, in which it is inserted; being adherent by its surface and its edges to the internal periosteum of the labyrinth.

The stapes accordingly forms a kind of movable lid or piston-head occupying the orifice of the fenestra ovalis, and capable of transmitting directly to the fluid of the labyrinth the impulses received from the membrana tympani. The extent of inward and outward movement of the base or footpiece of the stapes has been determined by Helmholtz in the following manner. The cavity of the tympanum and that of the vestibule having both been opened from above, the point of a fine sewing needle was inserted into the fibrous covering of the base of the stapes from the side of the vestibule, and the needle allowed to rest, near the point of its insertion, upon an adjacent edge of bone. It thus formed a kind of index-lever, which would indicate by the displacements of its long arm, very slight movements of the stapes. The stapes was then pressed inward and outward, as freely as its attachments would allow, either by means of a needle applied to the bone itself, or by alternately condensing and rarefying the air in the external auditory meatus; the force, in the latter case, being transmitted through the membrana tympani and chain of bones. The same observer estimated these movements according to another plan, by opening the superior semicircular canal of the labyrinth, and inserting into it a slender glass tube of known calibre, a portion of which, as well as the cavity of the vestibule, was filled with water. Any inward pressure upon the stapes would accordingly be indicated by a corresponding rise of the level of water in the tube. The movement of the stapes, in these experiments, varied, according to circumstances, from .025 to .072 millimetre.

The change of position of the stapes in the fenestra ovalis, due to the impulses received through the chain of bones, is not a simple sliding movement of advance and recession, but a rocking motion, in which its upper border is tilted over toward the cavity of the vestibule and back again, and its anterior end moves more freely than its posterior. This feature of the action of the stapes, which has been described by several observers, is shown by Helmholtz to depend upon the varying compactness of its fibrous attachments; these attachments being closer along its inferior border and at its posterior end, thus allowing more freedom of movement above and in front than below and behind.

The position of the stapes is also regulated by the action of the *stapedius* muscle. This muscle, the smallest in the body, arises from a bony canal behind the cavity of the tympanum; and its slender tendon, after entering this cavity, passes almost directly forward and is inserted into the posterior side of the neck of the stapes, near its articulation with the incus. Its contraction will, therefore, draw the angle of the stapes backward and its anterior extremity outward from the fenestra ovalis.

Physiological Action of the Chain of Bones and the Muscles of the Middle Ear.—The cavity of the tympanum is an irregularly shaped space, inside the membrana tympani, filled with air, across which the vibrations received by the membrane from without are transmitted by the chain of bones. In their natural position and with their natural

tendinous connections undisturbed, these bones are held in such close connection with each other that they vibrate as a single solid body.

The vibratory movement of the ossicles of the ear has no immediate dependence upon the action of the muscles attached to them, but results from the shocks received by the tympanic membrane. The influence of the muscles is to increase or diminish the tension of this membrane, and thus to influence the mode of transmission of the sound.

The action of the internal muscle of the malleus, or *tensor tympani*, is beyond doubt, as its name indicates, to increase the tension of the membrana tympani. It has long been known that, on opening the canal in which this muscle is lodged, as well as the cavity of the tympanum, by drawing upon its tendon within the canal, the membrana tympani may be manifestly rendered more tense; and according to Helmholtz, all the ligaments holding the ossicles in place are at the same time put upon the stretch.

The effect produced upon the act of hearing by increased tension of the membrana tympani has been interpreted in a different sense by different observers. Savart,[1] who first studied systematically the vibrations induced in stretched membranes by the proximity of sounding bodies, estimated the extent of these vibrations by the agitation of particles of fine sand spinkled on the surface of the membranes; and he found the vibrations more difficult of production, other things being equal, when the tension of the membrane was increased. He applied the same mode of experimentation to the membrani tympani in the ear of man and animals, and found not only that sand, sprinkled on its surface, would be thrown into agitation by holding near it a sounding body, but that also, as in the former case, these appearances were less easy of production when the membrane was rendered more tense by traction upon the tensor tympani muscle. He concluded from that, that during life the ear is more susceptible to sounds of a given intensity when the membrana tympani is relaxed, and less so when it is put upon the stretch; the tensor tympani, accordingly, exerting a protective action by lessening the apparent intensity of very loud sounds.

This view has been adopted by many eminent authors, owing in great measure to the valuable experiments of Savart. But this observer was not aware of an important fact which has been established by subsequent investigations, namely, that stretched membranes, like cords, cannot respond indiscriminately to sounds of every grade of tone, *but only to a certain number of these tones, which are separated from each other by definite intervals;*[2] and they will respond to a different set of tones only after their tension has been increased or diminished. In order, therefore, that a membrane may be easily thrown into induced vibration, its tension must correspond in a certain ratio with the tone of the sound produced.

[1] Journal de Physiologie. Paris, 1825, tome iv. p. 205.

[2] Daguin, Traité élémentaire de Physique. Paris, 1867, tome i. p. 596.

These considerations have induced a different view of the action of the tensor tympani in modifying the sensations of sound. With the membrane in a state of moderate tension, a certain proportion of tones only are distinctly appreciated, while the remainder are either inaudible or imperfectly transmitted to the internal ear. This is the state in which sounds generally are received by the organ of hearing, without exact appreciation of their relative pitch. But when the ear follows distinctly successive tones of varying pitch, or when it listens intently for a particular note, the tension of the membrana tympani is increased or diminished to such a degree as will enable the vibration to be transmitted with the most complete distinctness by the chain of bones to the fluid of the labyrinth. With regard to the modifications induced in the apparent *intensity* of sound, it is probable that Savart's explanation holds good; and that a diminished tension of the membrane enables the ear to catch more readily sounds which are faint or distant. This partial relaxation is accomplished by the action of the stapedius muscle, which is animated directly by a filament of the facial nerve; while the tensor tympani is supplied only from the otic ganglion of the sympathetic.

The cavity of the tympanum is not hermetically closed, but communicates with the pharynx by means of the *Eustachian tube*. The existence of this opening secures the equality of atmospheric pressure within and without the membrana tympani, a condition which is essential to its proper vibration under the influence of sonorous impulses. The external barometric pressure varies from day to day, and even for different periods of the same day; and if the middle ear were a closed cavity, this variation would of itself change the tension of the membrana tympani, independently of the action of the muscles. Although the mucous surfaces of the Eustachian tube are habitually in contact with each other, they readily yield to a preponderance of atmospheric pressure in either direction, and thus the equilibrium is maintained between the air inside and outside the cavity of the tympanum.

Labyrinth.—The internal ear, or labyrinth, so called from the complicated extension and windings of its various cavities and passages, is situated in the petrous portion of the temporal bone. Its external wall consists of a thin lamina of compact osseous tissue, which is readily isolated in the fœtus and in newly born infants, owing to its being immediately surrounded by spongy tissue; while in the adult it is more or less completely consolidated with the adjacent bony parts. It may be divided physiologically into: 1. The *vestibule and semicircular canals*, which constitute its most essential parts and are present in all vertebrate animals; and 2. The *cochlea*, which, in man and the mammalia, is a more highly developed portion, of complicated structure, but which is absent in the fishes and naked reptiles, and only partially developed in the scaly reptiles and in birds.

The *vestibule* (Fig. 211,1) is so called because its cavity is that into which the fenestra ovalis immediately opens, and from which those of

Fig. 211.

BONY LABYRINTH OF THE HUMAN EAR, twice the natural size.—1. Vestibule. 2. Superior vertical semicircular canal. 3. Inferior vertical semicircular canal. 4. Horizontal semicircular canal. 5. Fenestra ovalis. 6. Fenestra rotunda. 7. Cochlea.

the semicircular canals and cochlea diverge in various directions. It is of a more or less ovoid form, and presents, toward the cavity of the tympanum, two openings, namely: 1. The fenestra ovalis (5), corresponding in form to the base of the stapes, which nearly fills it, and which is adherent to the internal periosteum of the labyrinth stretched across the opening; and 2. The fenestra rotunda (6) of smaller size and closed only by a fibrous membrane. The posterior portion of the vestibule gives origin to the three semicircular canals, which communicate with its cavity at each extremity, namely: 1. The superior vertical canal (2) the plane of which is directed across the longitudinal axis of the petrous bone. 2. The inferior vertical canal (3) the plane of which is parallel with the internal surface of the petrous bone; and 3. The horizontal canal (4) which is directed across the axis of the petrous bone, but lies, as its name indicates, in a horizontal plane. Each semicircular canal opens into the vestibule by two orifices, one at each end; except that the two vertical canals unite at one of their extremities into a branch and orifice common to both. Thus there are five orifices leading from the vestibule into the three semicircular canals; and each canal has free communication at each end, directly or indirectly with the interior of the vestibule. Each canal is enlarged at one of its extremities where it joins the vestibule, into a slightly rounded dilatation.

The common cavity of this part of the bony labyrinth contains a limpid, colorless fluid, the perilymph, and, in addition, a closed membranous sac, also filled with fluid, which, by its various prolongations, presents a repetition of the form of the vestibule and semicircular canals. This, together with its extension in the cochlea hereafter to be described, constitutes the *membranous labyrinth*. It forms the most important part of the internal ear, since in its walls the filaments of the auditory nerve have their terminal distribution.

The cavity of the vestibule contains two membranous sacs, lying in contact with each other, but separated by a transverse partition. One of these, the smaller of the two, is the *sacculus*, a spherical vesicle, a little over 1.5 millimetre in diameter, occupying the anterior and inferior portion of the vestibule, and communicating by a narrow canal with the ductus cochlearis of the cochlea. The other, or larger sac, is the *utricle*, of ellipsoid form, measuring 3.5 millimetres in its long diameter. The utricle and the three membranous semicircular canals communicate with each other in the same way as the corresponding bony cavities in which

they are lodged. Each membranous semicircular canal presents at one of its extremities, at the expanded part of its bony canal, a similar rounded dilatation, known as the "ampulla."

The membranous sacs and semicircular canals are considerably smaller than the osseous cavities which contain them, and occupy nearly everywhere an eccentric position; being, at certain points, in contact with and adherent to the internal periosteum, while at others they are surrounded by the perilymph. The sacculus and utricle together occupy about two-thirds of the cavity of the vestibule; and, according to Rüdinger, are so placed that neither of them touches the base of the stapes at the fenestra ovalis, but are separated from it by an appreciable layer of fluid. Thus the sonorous impulses which reach the membranous labyrinth come to it, not directly from the stapes, but through the intermediate vibration of the perilymph.

The sacculus and the utricle are adherent to the internal periosteum of the vestibule at the points of entrance of their corresponding branches of the auditory nerve. The ampullæ of the semicircular canals fill almost completely the bony cavities in which they rest, their outer surface lying for the most part in contact with the periosteum. On the other hand, the membranous semicircular canals are very much smaller in calibre than the osseous excavations which contain them, and lie in contact with the periosteum only along the inner or smaller curvature of the bony canals; so that they are surrounded externally by a comparatively large quantity of perilymph. They are, however, attached and held in place, as shown by Rüdinger, by slender, scattered, fibrous bands and partitions, which traverse at various points the perilymphic space.

The main point of interest in regard to the membranous labyrinth relates to the mode of *distribution and termination of the auditory nerve.*

The auditory nerve sends to the vestibule two branches; one of which is distributed to the sacculus, the other to the utricle and ampullæ. The mode of termination of the nerve fibres in both these divisions is essentially the same. They are not distributed generally over the membrane, but terminate only in particular well-defined spots, characterized by a thickening or prominence of the membranous wall, and by the presence of a peculiar form of epithelium provided with stiff, pointed cilia, the so-called *auditory hairs.*

In the sacculus and in the utricle, the terminal nerve spot, or "macula auditiva," is in the form of an oval plate, or lamina, 3 millimetres by 1.5 in the sacculus, and 3 millimetres by 2 in the utricle. In the ampullæ, it forms a transverse ridge or fold of the membranous wall, projecting inward after the manner of the valvulæ conniventes of the small intestine, but occupying only about one-third of the circumference of the ampulla. Elsewhere, the membranous sacs of the labyrinth are lined, according to Kölliker, by a single layer of pavement epithelium cells. But at the spots in question the epithelium is twice or three

times as thick as in the remaining portions, and consists of elongated cells of two different forms, namely, cylindrical and fusiform. It also presents, standing upright upon its free surface, the pointed cilia above mentioned, or auditory hairs, which in man are about 25 mmm. in length. The terminal nerve fibres of the auditory nerve, which pass up toward these thickened spots of epithelium, may be traced, according to the testimony of all recent observers, into the epithelial layer itself; and certain appearances give rise to the supposition that the ultimate axis-cylinder of each nerve fibre is prolonged through the substance of a fusiform epithelium cell, and finally becomes the cilium or auditory hair projecting from its free extremity. These appearances are, 1st, the similarity in size and aspect between the axis-cylinder of the nerve fibres and the slender downward prolongations of the fusiform cells; and, 2d, the fact that both these structures become stained more or less deeply of a blackish or brown color by the action of osmic acid (Rüdinger). Whatever the precise relations of the terminal nerve fibres to the other elements of the epithelial layer may be, there is no doubt that the projecting cilia act either mechanically, or by virtue of a real nervous sensibility belonging to them, and are the immediate recipients of the sonorous vibrations communicated by the surrounding fluid.

A remarkable secondary feature connected with the auditory spots of the sacculus and utricle is the existence, at each, of a deposit of minute solid calcareous grains, the so-called *otoconia*, or ear sand. These grains are embedded in a homogenous gelatinous material, and form a white chalky-looking layer immediately over the auditory spot, by which the situation of this spot is easily recognized. The grains are composed almost exclusively of lime carbonate. They are rounded, elongated, or distinctly prismatic and crystalline in form; the largest measuring, according to Kölliker, about 10 mmm. in length. The exact office performed by these calcareous deposits is unknown, but it is evident from their constant existence in the same situation in different animals, that they have some important relation to the sense of hearing. In mammalians and birds they are pulverulent, as in man. In reptiles and fish they assume the form, sometimes, of friable chalky concretions, sometimes of rounded masses of considerable size, hard and dense as porcelain. According to Wagner, they are completely absent only in the cyclostomi, or lowest order of true fishes, including the lamprey and the hag.

Physiological Action of the Membranous Labyrinth.—The sacculus and utricle, contained in the cavity of the vestibule, are membranous formations, to which the fibres of the auditory nerve are distributed, and in which they terminate. These membranous expansions are supported by the contact of fluid on each side, and are held in place by the partial fibrous attachments which connect them with the wall of the vestibule. They are the structures upon which the impressions of sound are finally received, and correspond, in this respect, to the retina in the organ of

vision. The sonorous impulses, first communicated by the atmosphere to the membrana tympani, are thence transmitted through the bony tissue of the malleus, incus, and stapes. From the base of the stapes they pass to the perilymph of the vestibular cavity ; from that, through the floating wall of the membranous sac, to the endolymph or the fluid contained in its interior ; and it is the vibration of this internal fluid which finally acts upon the sensitive nervous terminations in the auditory spot. It is thus through a series of intermediate vibrations, that sounds coming from the exterior produce their impression upon the internal ear.

Office of the Semicircular Canals.—These singular appendages of the bony and membranous labyrinth have attracted attention, especially on account of the constancy of their occurrence and the peculiarity of their position. The principal features of their anatomical history are the following :

1. They are universally present, as portions of the internal ear, in mammalians, birds, and reptiles, and nearly always in fish ; being entirely absent only in amphioxus, where there is no organ of hearing whatever.

2. They are always three in number. The only exception to this rule is found among fishes, in the lamprey and the hag ; where the entire structural development, especially in the organs of sense, is very incomplete.[1] In the lamprey there are two, and in the hag one only, the cavity of which is confounded with that of the utricle ; the whole forming a membranous canal bent upon itself like a ring.

3. The three canals stand in three different planes, which are all perpendicular to each other. Thus one is vertical and longitudinal, in respect to the axis of the petrous bone ; another vertical and transverse; and the third transverse and horizontal. They represent accordingly, by their position, the three dimensions of space ; and from this circumstance the idea was early suggested that they might serve in some way to indicate the direction in which sounds arrive from the exterior. But subsequent researches have yielded nothing to corroborate this assumption ; and it is evident, furthermore, that, from whatever quarter sonorous impulses originally come, they must traverse the membrana tympani and chain of bones, and finally reach the internal ear by the same course. This view of the office of the semicircular canals is therefore no longer entertained.

Lastly, an essential point in their anatomical structure is that they are destitute of nerve fibres, and consequently are wanting in sensibility. The only nervous distribution connected with them is that to the ampullæ situated at one of their extremities, but no nerve fibres extend to the semicircular canals themselves. The function which they perform must therefore in all probability be one of a mechanical or physical kind.

[1] Owen, Anatomy of the Vertebrates. London, 1868, vol. iii. p. 222. Wagner, Comparative Anatomy of the Vertebrate Animals, Tulk's translation. New York, 1845, p. 227.

In experimenting upon the internal ear in the lower animals, it has been remarked that division or injury of the semicircular canals is followed by a singular alteration in the position and movements of the animal, indicating a disturbance of equilibrium. These phenomena were first made known by Flourens in 1825,[1] and have been corroborated by many subsequent observations, the most recent being those of Cyon, Curschman, Bœttcher, and Berthold, in 1874. The results met with are not explained in the same way by all experimenters, but there is little discrepancy in regard to the phenomena actually presented. The operation of exposing the semicircular canals during life is impracticable, as a general rule, in the mammalia, owing to the density of the petrous bone in which they are imbedded; but it can be done without much difficulty in birds, where they are surrounded only by a loose and spongy osseous tissue. The pigeon is the species which has been most frequently used for this purpose.

The most striking and constant effect produced by injury of the semicircular canals consists of abnormal oscillatory movements of the head, together with an imperfect balancing of the whole body These phenomena vary according to the particular canal which has been divided. If a vertical canal be the one injured, the oscillation of the head is upward and downward; if it be a horizontal canal, the oscillations are lateral, from left to right, and *vice versâ.* If the two corresponding canals on both sides be divided, the abnormal movements are much more rapid and continuous than if the injury be inflicted on one alone. The animal is still capable of preserving the equilibrium of the body, so long as he remains at rest; but any attempt at movement brings on a disorder of muscular action which makes walking, running, or flying difficult or impossible. The most simple interpretation of these results is that the animal can no longer appreciate the direction or extent of the changes in position of the head, and that the sense of equilibrium is consequently impaired for movements of the body and limbs.

The manner in which the semicircular canals, in their natural condition, may be regarded as contributing to the sense of equilibrium, is as follows: If a glass goblet, filled with water, be turned round its vertical axis, it will be seen that the water does not readily turn with it; and any small objects suspended in it, or floating upon its surface, will remain in nearly the same position, while the goblet revolves through an entire circle. The adhesion of the fluid to the sides of the glass vessel is not sufficient to communicate to it at once the circular motion of the parts with which it is in contact. Consequently the water lags behind the glass; and if any flat object were cemented perpendicularly to the inside of the goblet, so as to turn with it, it would be subjected to a backward pressure from the water, whenever the goblet were put in rotation.

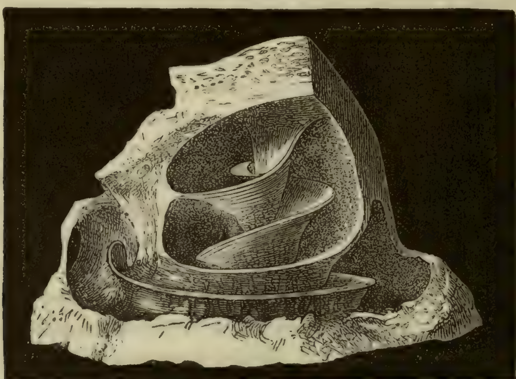
[1] Recherches Expérimentales sur les Propriétés et les Fonctions du Système Nerveux, 2me édition. Paris, 1842, pp. 452, 454.

Somewhat similar conditions are present in the semicircular canals. Whenever the head is rotated from side to side in a horizontal plane, a momentary increase of pressure must take place in the fluid of the horizontal semicircular canal (Fig. 211, 4), either toward or from the ampulla at one end; and this increase or diminution of pressure may be preceptible by the nervous expansions which are situated there. If the head be moved upward or downward, a similar variation of pressure will take place in the inferior vertical canal (Fig. 211, 3); and if it be inclined laterally, toward the right or left shoulder, the superior vertical canal (Fig. 211, 2), will experience a variation of the same kind. Thus, although the membranous semicircular canals be not themselves sensitive to pressure, they may serve as channels for conducting an impulse to the sensitive organs in their ampullæ. Even the peculiar configuration of the nervous expansions in the ampullæ seems especially adapted for this purpose; since they are arranged in the form of transverse crescentic folds, while in the sacculus and utricle they are simply flattened prominences on the inner surface of these cavities.

If the question be asked, why an apparatus for appreciating changes of equilibrium should be especially associated with the organ of hearing, it may be remarked that in the auditory labyrinth alone there is to be found a terminal distribution of sensitive nerve fibres in an epithelium provided with hair cells, and surrounded by a fluid of watery consistency; all of which conditions are suitable for the perception both of sonorous vibrations and of the variation in pressure due to changes of position.

Cochlea.—The cochlea, named from its external resemblance to a snail-shell, is a bony canal rolled spirally about a central axis, and

Fig. 212.



BONY COCHLEA OF THE HUMAN EAR, right side; opened from its anterior face. (Cruveilhier.)

making between two and three turns upon itself. Owing to the gradual rise of the turns, it has a slightly conoidal form, the extremity of which, or cupola, is directed forward, downward, and outward. The canal of

the cochlea is divided longitudinally into two parts by a thin, bony partition, the *spiral lamina*, which winds round its bony axis, following its spiral turns, but limited externally by a free border.

From the free border of the bony spiral lamina a fibrous membrane, the *membrana basilaris*, extends outwardly quite to the external wall of the cavity, to which it is attached. The common canal of the cochlea is thus divided into two parallel passages or stairways, one above the other. The superior of these passages communicates freely at its base with the cavity of the vestibule, and is the *scala vestibuli*. The inferior reaches to the fenestra rotunda, and is terminated by the membrane stretched across this opening, which alone divides its cavity from that of the tympanum; it is accordingly known as the *scala tympani*. Both these canals extend, in their spiral course, to the summit or cupola of the cochlea. At this point a minute orifice of communication between the two has been described by some writers, and doubted by others. According to the observations of Buck,[1] it is probable that no such opening exists in the natural condition of the parts, unless it be microscopic in size. But whether the two canals communicate or not, at the summit of the cochlea, the partition between them, throughout their parallel course, is partly membranous; and by this means an increase or diminution of pressure upon the fluid of the vestibule at the fenestra ovalis will be at once transmitted, through that of the scala vestibuli and the scala tympani, to the membrane of the fenestra rotunda. Notwithstanding, therefore, the incompressible character of the fluid of the labyrinth, provision is made, to a certain extent, for the movement of the stapes, according to the contraction or relaxation of the muscles of the middle ear.

But the septum above described, formed by the spiral lamina and the membrana basilaris, is not the only longitudinal partition in the cavity of the cochlea. The scala vestibuli is also divided into two parallel canals, an internal and an external, by a thin membranous sheet which starts from the upper surface of the spiral lamina near its outer border, and extends upward and outward to reach the external wall of the cochlear cavity. As this membrane leaves the plane of the spiral lamina and membrana basilaris at an angle of about 45 or 50 degrees, it shuts off from the scala vestibuli a separate canal of prismatic form, having for its floor the membrana basilaris, for its outer wall the wall of the cochlea, and for its upper boundary the oblique membranous partition between it and the scala vestibuli. This canal contains the auditory epithelium cells and the termination of the fibres of the auditory nerve. It is therefore the essential part of the cochlea, and is termed accordingly the *ductus cochlearis*.

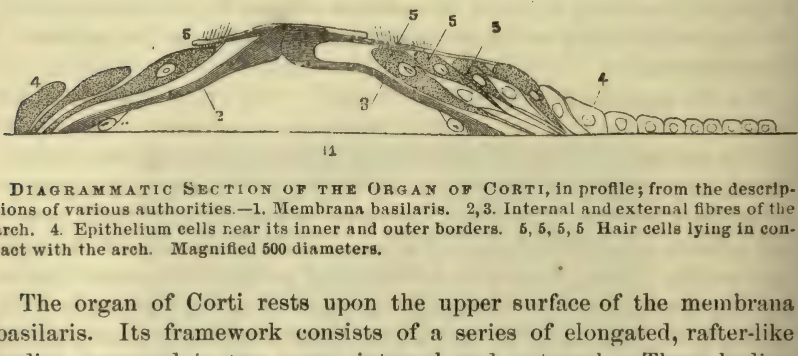
The ductus cochlearis terminates at the summit of the cochlea by a

[1] On the Mechanism of Hearing, Prize Essay of the Alumni Association of the College of Physicians and Surgeons, New York. Published in the *New York Medical Journal*, March, 1874.

blind extremity; but at its base it communicates, by a narrow channel, with the cavity of the sacculus. It is consequently an extension of the sacculus, and a part of the membranous labyrinth; while the scala vestibuli is only an extension of the general cavity of the vestibule. The ductus cochlearis may be considered as a tubular prolongation of the sacculus, rolled upon itself in a spiral form, and maintained in position by the bony and membranous partitions of the cochlea by which it is enveloped. Like the rest of the membranous labyrinth, it is filled with a watery fluid, and is bathed externally on both sides by the perilymph, except where it is adherent to the walls of its bony cavity.

Organ of Corti.—The inner surface of the ductus cochlearis is lined for the most part with a thin layer of pavement epithelium, except along a longitudinal line situated at about the middle of the membrana basilaris. Here there is a continuous elevated ridge, four or five times thicker than the epithelium elsewhere, following a spiral course, like the rest of the cochlear structures, and consisting of enlarged and modified epithelium cells, with the terminal fibres of the auditory nerve. This body is termed the *organ of Corti*, from the name of the observer who first described it in 1851.[1] It is justly considered as the most remarkable and complicated structure in the internal ear, although in its essential features it is analogous to the auditory spots in the sacculus and utricle.

Fig. 213.



DIAGRAMMATIC SECTION OF THE ORGAN OF CORTI, in profile; from the descriptions of various authorities.—1. Membrana basilaris. 2, 3. Internal and external fibres of the arch. 4. Epithelium cells near its inner and outer borders. 5, 5, 5, 5 Hair cells lying in contact with the arch. Magnified 500 diameters.

The organ of Corti rests upon the upper surface of the membrana basilaris. Its framework consists of a series of elongated, rafter-like bodies, arranged in two rows, internal and external. These bodies, the internal and external "fibres of Corti," are separated from each other at their base, where they rest upon the membrana basilaris, by a considerable interval; but they lean toward each other and lie in contact by their upper extremities or heads, thus forming a roof-like or arched connection, the "arch of Corti." Near the situation of the arch of Corti, the epithelium cells lining the ductus cochlearis become modified in form, gradually increasing in size and length. At the inner border of the arch there is a single row of epithelium cells which are nearly as long

[1] Zeitschrift für Wissenschaftliche Zoologie. Leipzig, 1851, Band III. p. 109.

as the internal fibres of Corti, and which lie immediately next to them in a similar leaning position. The upper extremity of each of these cells bears a tuft of rigid hairs or cilia, which are analogous to those of the hair cells of the sacculus and utricle. On the outside of the arch there are three such rows of hair cells, and in every instance the tufts of cilia project through openings in a sort of fenestrated cuticle which lies above the cells, and extends over them, inward and outward, from the heads of the two bodies forming the arch of Corti.

The terminal fibres of the cochlear branch of the auditory nerve are distributed to the organ of Corti. The bundles of nerve fibres forming this branch penetrate the cochlea at the base of its central axis, and pass from below upward through its interior, diverging successively from within outward, to continue their course in a horizontal direction between the two layers of the spiral lamina. At the level of the attached border of the spiral lamina there is situated, within the cavity of the osseous canal, a linear collection of bipolar nerve cells, in and among which the nerve-fibres pass, and with many, if not all, of which the nerve fibres are directly connected. This forms the "spiral ganglion" of the cochlear nerve. After the bundles of nerve fibres have passed through the ganglion, and while they are contained in the thickness of the spiral lamina, they form, by repeated subdivision and reunion, a complicated plexus, the filaments of which continue however to follow a general diverging course toward the outer border of the spiral lamina and the attached edge of the membrana basilaris. Arrived at this point, the nerve fibres diminish in diameter and lose their medullary layer; and, in this form, penetrate into the ductus cochlearis, where they continue to radiate toward the organ of Corti. It is at this situation that the final termination of the slender and pale nerve fibres in the substance of the epithelial hair cells has been most positively described and figured by Waldeyer.[1] There can be no doubt that this structure represents, in the ductus cochlearis, the especial organ of auditory sensibility.

Physiological Action of the Cochlea.—The cochlea is undoubtedly that part of the internal ear, which, as compared with the remainder, serves for the more precise discrimination of minute variations in sound. Its elongated and spiral form, the two membranes of uniform tension which inclose the ductus cochlearis above and below, and the remarkable complication of structure, with the multiple rows of hair cells belonging to the organ of Corti, all indicate that it is adapted for the distinct perception of particular sonorous impulses. The analogy of its construction in some respects with the mechanism of a musical stringed instrument, the fibres of the membrana basilaris representing its vibrating strings, has induced the belief, in the minds of many eminent physiologists, that it is the organ by which we appreciate the difference in tone or pitch between different sounds. According to this view, the radiating fibres

[1] In Stricker's Manual of Histology, Buck's edition. New York, 1872, p. 1040.

in successive portions of the membrana basilaris are attuned, by their length or tension, to vibrate in response to different notes of the musical scale; and the vibration of each set, when excited, is communicated to the corresponding hair cells of the organ of Corti, and thus reaches the auditory nerve fibres terminating in their substance. Thus for every note sounded in the atmosphere which gains admission to the internal ear, only certain fibres and hair cells of the ductus cochlearis will be thrown into vibration, and only certain terminal fibres of the cochlear nerve will receive a sonorous impression. Some writers have even found in certain parts of the organ of Corti, an apparatus for damping the vibration of the fibres after the cessation of the sound, and thus preventing the confused intermingling of separate impressions. There is certainly a suggestive appearance of similarity between the long row of fibrous and cellular elements in the organ of Corti, with their various appendages, and the ranges of strings, capable of vibrating to different notes, in a harp or piano forte; and the similarity is sufficient to suggest a certain correspondence of mechanical and physiological action between the two.

But the main difficulty in attributing to the cochlea, as its function, the discrimination of musical notes, lies in the fact that its development in different animals does not correspond with their capacity for the production and perception of musical sounds. The cochlea, under the form which it presents in man, is confined to the mammalia. In birds this part of the auditory apparatus has not the form of a coiled spiral, but is an obtusely conical eminence,[1] containing two small cartilaginous cylinders united by a membrane which represents the membrana basilaris; and the part corresponding to the organ of Corti contains only nerve terminations and hair cells somewhat resembling those of the inner row in mammalia; the arch of Corti, and the three outer rows of hair cells, with their cuticular covering, being absent. In serpents and lizards, the cochlea is similar to that of birds; while in the naked reptiles and in fishes it is completely undeveloped.

Thus, in all the mammalia, the cochlea is an important part of the internal ear, apparently but little, if at all, inferior to the same organ in man. But in the singing birds it is comparatively a rudimentary structure. Some of these birds may be taught artificially to repeat particular melodies, showing conclusively that their capacity of perception for musical notes is equal to their power of producing them by the vocal organs. And yet that part of the auditory apparatus which should be most highly developed in these animals, according to the view in question, is in reality the least so. If we compare, for example, a horse or a pig with a thrush or a mocking-bird, it is evident that the grade of musical sensibility in these animals is in no relation with the

[1] Owen, Anatomy of the Vertebrates. London, 1866, vol. ii. p. 134. Wagner, Comparative Anatomy of the Vertebrate Animals, Tulk's Translation. New York, 1845, p. 95. Waldeyer, in Stricker's Manual of Histology, Buck's Edition. New York, 1872, p. 1046.

development of the cochlea. In fact, the cochlea of a singing bird resembles that of a crocodile or a serpent more closely than that of a quadruped or a man. At the same time, the other parts of the internal and middle ear in birds, the double sac of the vestibular cavity, the membranous semicircular canals and ampullæ, the fenestra ovalis and rotunda, the chain of bones and the membrana tympani, are all highly developed; some of them nearly or quite as much so as in the mammalian class. These facts throw a certain degree of doubt upon the special office of the cochlea in the perception of auditory sensations.

Persistence of Auditory Impressions and the Production of Musical Notes.—The sensation excited by a sonorous vibration continues for a short time after the cessation of its cause. Usually the interval between successive impulses is more than sufficient to allow the continued impression to disappear, and the ear distinguishes without difficulty the succession of sounds. But if the impulses follow each other at equal intervals, and with a certain degree of rapidity, they produce upon the ear the impression of a continuous sound, and this sound has a higher or lower pitch according to the rapidity with which the vibrations are repeated. The numerical relation of different musical notes thus produced has been studied by means of various instruments. One of these is the *siren* of Savart, in which successive puffs of air are emitted from the body of the machine through small openings, with a degree of rapidity which can be varied at will and registered by an index attached to the moving parts. Another method is that in which the shocks are given by the points of a toothed wheel turning with known velocity, and striking, in their passage, against the projecting edge of a card. In another modification of the same plan, the revolving wheel carries one or more projecting rods, which pass, in succession, through a corresponding slit in a stiff board; making at each transit an atmospheric concussion, owing to the instantaneous displacement and rebound of the air at the opening. Finally, the number of vibrations corresponding to a particular note may be registered by attaching to the extremity of a diapason, or tuning-fork, a light stilet which traces upon the blackened surface of a cylinder, revolving at a known rate, an undulating line (Fig. 146, *a*); the number of undulations within a given space indicating the frequency of the vibrations of the tuning-fork. A *simple* vibration represents the single oscillation of a solid body, or the particles of a fluid, in one direction; a *double* vibration is the complete to-and-fro movement of a particle, which brings it back to its original position.

By this means it is found that sonorous impulses, which follow each other with a rapidity of less than sixteen times per second, are readily distinguishable as separate shocks; but above that degree of frequency they become merged into each other, and produce the sensation of a continuous sound. In case the repetition of the shocks takes place at irregular or unequal intervals, the only characters perceptible in the sound are its intensity and the peculiarities due to the special

mechanism of its production. But if the shocks succeed each other at regular intervals, the sound has then a definite position in the musical scale, and is appreciated by the ear as a high or low note. The more frequent the repetitions in a given time, the higher is the note produced, until a limit is reached at which the ear fails to perceive a sound at all. The physical reason why excessively high notes become inaudible is probably this: In the special arrangement of the auditory apparatus, a vibration, in order to be perceptible, must have a certain degree of extent or amplitude; that is, the particles of the vibrating body must move to and fro, at each impulse, for a certain distance in space. The intensity of a sonorous impression, accordingly, depends upon the amplitude of the vibrations, while its pitch or tone depends upon their frequency. But the more frequently a body vibrates in a single second, the less extensive must be its movements, if their velocity remain the same. Consequently, when these vibrations arrive at a certain high degree of frequency, unless the velocity of movement can be increased in proportion, their amplitude becomes so small that they can make no impression upon the ear, and the sound becomes inaudible.

It is evident, however, that such a sound would be perceptible if the sensibility of the auditory apparatus were increased to the requisite degree; and it has been suspected by some naturalists that certain insects may be capable of perceiving sounds of so high a pitch as to be inaudible for the human ear; while, on the other hand, for them, a very low note would appear as a succession of distinct impulses.

The limits of frequency, within which sonorous vibrations are perceptible to man as continuous musical sounds, are 16 double vibrations per second for the lowest notes, and 38,000 for the highest. But, according to Wundt, the exact discrimination of the pitch of musical sounds is confined within much narrower limits, especially for the higher notes.

Duration of a Sound required for the perception of Sonorous Impressions.—This point has been investigated by Savart[1] in the following manner. He ascertained, by experiment, that the ear could appreciate the pitch of a sound made by a toothed wheel revolving at such a rate as to cause 10,000 shocks per second. By removing successively the teeth from larger portions of the circumference, he diminished in a corresponding degree the time during which the shocks were produced; and he found that such a wheel would give a sound of definite pitch with only two adjacent teeth remaining. The double shocks thus produced would occupy only $\frac{1}{5000}$ of a second; and this duration of the impulses was sufficient to make upon the ear a distinct musical impression.

[1] Daguin, Traité Elémentaire de Physique. Paris, 1869, tome i. p. 517.

SECTION III.

REPRODUCTION.

CHAPTER I.

THE NATURE OF REPRODUCTION, AND THE ORIGIN OF PLANTS AND ANIMALS.

Reproduction is the process by which the different kinds of organized bodies are perpetuated in continuous series, notwithstanding the limited term of existence allotted to each individual. It includes the phenomena of the production, growth, and development of new germs, as well as the whole history of the successive changes in the organs and functions, and the consequent modifications of external bodily form presented at different periods of life.

All organized bodies pass through certain successive stages of development, in which their structure and functions undergo corresponding alterations. The living animal or plant is mainly distinguished from inanimate substances by the continuous changes of nutrition and growth which take place in its tissues. These nutritive changes correspond in activity with the other vital phenomena; since the production of these phenomena depends upon the regular and normal continuance of the nutritive process. Thus the organs and tissues, which are the seat of a double change of renovation and decay, retain nevertheless their original constitution, and continue capable of exhibiting the vital phenomena.

These changes, however, are not the only ones which take place. Although the structure of the body appears to be maintained in an unaltered condition by the nutritive process from one moment to another, or from day to day, yet a comparative examination at greater intervals of time will show that this is not precisely the case; but that the changes of nutrition are, in point of fact, progressive as well as momentary. The composition and properties of the skeleton are not the same at the age of twenty-five years that they were at fifteen. At the later period the bones contain more calcareous and less organic matter than before; and their solidity is increased, while their elasticity is diminished. Even the *anatomy* of the bones alters in an equally gradual manner; the medullary cavities enlarging with the progress of growth,

and the cancellated tissue becoming more open in texture. There is a notable difference in the quantities of oxygen and carbonic acid inspired and exhaled at different ages. The muscles, also, if examined after the lapse of some years, are found to be less irritable than formerly, owing to a slow, but steady and permanent deviation in their intimate constitution.

The vital properties of the organs, therefore, change with their varying structure; and a time comes at last when they are perceptibly less capable of performing their original functions than before. The very exercise of the vital powers is inseparably connected with the subsequent alteration of the organs employed in them; and the functions of life, instead of remaining indefinitely the same, pass through a series of successive changes, which finally terminate in their complete cessation.

The history of a living animal or plant is, therefore, a history of successive epochs or phases of existence, in each of which the structure and functions of the body differ more or less from those in every other. The organized being has a definite term of life, through which it passes by the operation of an invariable law, and which, at some regularly appointed time, comes to an end. The plant germinates, grows, blossoms, bears fruit, withers, and decays. The animal is born, nourished, and brought to maturity, after which he retrogrades and dies. The very commencement of existence, by leading through its successive intermediate stages, conducts at last necessarily to its own termination.

But while individual organisms are constantly perishing and disappearing from the stage, the particular kind, or *species*, remains in existence, without any important change in the appearance of the organized forms belonging to it. The horse and the ox, the oak and the pine, the different kinds of wild and domesticated animals, even the different races of man himself, have remained without any essential alteration since the earliest historical epochs. Yet during this period innumerable individuals, belonging to each species or race, have lived through their natural term and successively passed out of existence. A *species* may therefore be regarded as a type or class of organized beings, in which the particular forms composing it die off and disappear, but which nevertheless repeats itself from year to year, and maintains its ranks constantly full by the regular accession of new individuals. This process, by which new organisms make their appearance, to take the place of those which are destroyed, is known as the process of *reproduction*. The first important topic, in the study of reproduction, is that of the conditions necessary for its accomplishment.

Reproduction by Generation.—It is well known that, as a rule, in the reproduction of any particular kind of living organism, the young animals or plants are produced, directly or indirectly, from the bodies of the elder. The relation between the two is that of parents and progeny. The progeny, accordingly, owes its existence to an act of *generation;* and the new organisms, thus generated, become in turn the

parents of others which succeed them. For this reason, wherever such plants or animals exist, they indicate the preceding existence of others belonging to the same species; and if by any accident the whole species should be destroyed in any particular locality, no new individuals could be produced there, unless by the previous importation of others of the same kind.

The most prominent feature of generation, as a natural phenomenon, is that the young animals or plants thus formed *are of the same kind with their parents.* They reproduce all the essential specific characters by which their predecessors were distinguished; and this takes place by a law so universal that it seems almost a truism to state it. But this is only because it has been so constantly a matter of observation, that in popular experience it appears as a natural necessity. In reality it is one of the most remarkable phenomena connected with the generative process; and it indicates an unbroken connection of physiological acts, extending through the entire lives of many different individuals. Thus we know that the progeny of a fox will always be foxes; and that if we sow oats, it will be a crop of oats that is produced in consequence. Generation, accordingly, not only gives rise to new animals and plants, or increases their number, but it also serves to continue indefinitely the existence of the particular species, with all its characteristic marks and qualities.

Our idea, therefore, of a species, whether animal or vegetable, includes two different elements, one of which is anatomical, the other physiological. The anatomical character of a species consists in the similarity of form, size, and structure existing between all the individuals belonging to it, and which we recognize at a glance; its physiological character depends upon the fact, which has been learned by experience, that it will reproduce itself, and that the different species in existence at any one time remain distinct through an indefinite series of successive generations.

It is not possible to say that the anatomical characters of species have remained absolutely the same throughout all previous time, or that they will continue to do so without limit in the future. The existence of many fossil remains of animals and plants, different from those which are known at the present day, shows that species are not invariable and persistent through very long periods of time; and that they may either very gradually become so modified as to present a different appearance, or else that they may entirely come to an end, like the extinct mastodons and fossil horses of the United States, and be replaced by others from a different locality. But in whatever way the succession of species in different geological epochs be explained, it is certain that at any one period their essential physiological characters are those above described; and that each species, by the process of generative reproduction, remains distinct from the others which are contemporary with it.

But the production of young animals, similar in every respect to their

parents, although in all cases the final result of the generative process, is never immediate. The young progeny when first produced is different from its parents, and only reaches a condition of resemblance to them through a series of changes, often of a very extraordinary kind. In the vertebrate animals generally, the embryo, though quite incomplete in structure, yet presents a certain analogy of form with the adult condition. But in many of the invertebrate animals the young, even after hatching, and when capable of active locomotion, are so different in appearance from their parents that they would never be supposed to belong to the same species, unless their identity were demonstrated by their subsequent development. Thus the young mosquito is a wingless creature living beneath the surface of the water in stagnant pools; and the eggs of the butterfly, when hatched, give birth not to butterflies but to caterpillars. These caterpillars, however, are not creatures of a different species, but only young butterflies; and they become fully developed and similar to their parents after certain changes, which take place at definite periods of their development.

The reproduction or repetition, therefore, of the form which distinguishes a particular species is accomplished by a series of changes which follow each other in regular order; and this series, taken together, may be represented by a circuit, which starts from the egg, is continued through the different phases of growth, transformation and maturity of the animal, and terminates again with the production of an egg. As this egg is similar to the first, the changes repeat themselves in their previous order, and the indefinite continuance of the species is thus established.

Spontaneous Generation.—The commonest observation shows that the facts detailed above hold good in regard to all animals and plants with whose history we are familiarly acquainted. An opinion, however, has sometimes been entertained that there may be exceptions to this rule; and that living beings can, under certain circumstances, be produced from inanimate materials; presenting, accordingly, the singular phenomenon of a progeny without parents. Such a production of organized bodies is known by the name of *spontaneous generation*. Its existence is doubted by most physiologists at the present time, and has never been positively established for any particular organized species; but it has been at various periods the subject of active discussion, forming a somewhat remarkable chapter in the history of general physiology.

It may be remarked in general terms that the organisms, in regard to which the idea of the possibility of spontaneous generation has been entertained, have been always those whose natural history was imperfect or obscure, owing either to their minute size or to certain of their physiological peculiarities. Wherever animals or plants appeared in considerable abundance without exhibiting any evidence of the source from which they came, it was formerly conjectured, from that fact alone, that their production was a spontaneous one. The ancient naturalists

supposed that all species of animals, excepting those which visibly either laid eggs or produced living young, were formed spontaneously from the combination of their organic ingredients. Maggots, shell fish, grubs, worms, and even some fishes were thought to be produced in this way, simply because they had no apparent specific origin.

But continued observation in natural history showed that in these cases the animals were really produced by generation from parents; their secret methods of propagation being discovered, and their specific identity being established by successive changes in development of the young. The difficulty of doing this in any particular case is often increased by the interval which elapses between the deposit of eggs by the parents and the subsequent hatching of the young; the new generation not showing itself until after the former has disappeared. A similar instance is that of the American seventeen-year locust (*Cicada septendecim*), where a period of seventeen years intervenes between the hatching of the larva and the appearance of the perfect insect; the larva all this time remaining buried in the ground, while the life of the perfect insect does not last over six weeks. But notwithstanding this difficulty, all such doubtful cases were gradually traced to the usual method of generation from parents.

Another source of error was the great dissimilarity in the figure sometimes existing between the parents and their young, especially as this is accompanied by an equal dissimilarity in their habits of life. Until about the middle of the seventeenth century there was supposed to be no more undoubted instance of spontaneous generation than the appearance of maggots in putrefying meat. These creatures always show themselves in meat at a certain stage of its decomposition; they never appear elsewhere; and they do not themselves manifest the power of producing young: and for these reasons they were believed to originate from the dead flesh and to die themselves without leaving a progeny. But the simple experiments of Francisco Redi in 1668, demonstrated the source of fallacy in this opinion and the true origin of the maggots. He took, in the month of July, eight wide-mouthed glass bottles and placed in them various pieces of dead flesh. Four of these bottles were left open to the atmosphere, while the remaining four were closed by pieces of paper carefully adjusted over the mouth of each and fastened by a cord round its neck. A short time afterward the flesh in the uncovered bottles was filled with maggots, a peculiar kind of fly meanwhile passing in and out by the open mouth; but in the closed bottles not a single maggot was visible, even after the lapse of several months.

Thus it was evident that the maggots were not formed from the dead flesh, but that their germs came in some way from without; and continued observation showed that they were hatched from eggs deposited by the flies, and that after a time they became developed into perfect insects similar to their parents. An extension of these observations to other species of invertebrate animals made known a great variety of instances in which the connection of parents and progeny might be traced

through several intermediate conditions; so that the apparent difference between them in configuration and structure no longer offered a serious difficulty to the investigator. As a general rule, since that time, whenever a rare or comparatively unknown animal or plant has been suspected to originate by spontaneous generation, it has only been necessary to examine thoroughly its habits and functions, to discover its real methods of propagation, and to show that they correspond, in all essential particulars, with the ordinary laws of reproduction. The limits within which it is possible for the doctrine of spontaneous generation to be applied have been successively narrowed, in the same degree that the study of natural history has advanced; the presumption of its existence always hanging upon the outskirts of definite knowledge, and being connected only with those animal or vegetable organisms which are for the time imperfectly understood. The two groups from which it has been most recently excluded by the progress of discovery are, 1. The Entozoa, or internal parasites; and 2. The Infusoria.

I. *Entozoa.*—These are organisms which live within the bodies of other living animals, from whose organic juices they derive their nourishment.

There are many different kinds of entozoa, all of which are confined, more or less strictly, to certain parts of the body which they inhabit. Some of them are found in the intestines, others in the liver, the kidneys, the lungs, or the heart and bloodvessels; others on the surface of the brain; others even in the muscles or in the interior of the eyeball. Each particular kind of parasite, as a rule, is peculiar to the species of animal which it inhabits, and even to a particular part of the body, often to a particular part of one organ. Thus, Ascaris lumbricoides is found in the small intestine, Oxyuris vermicularis in the rectum, Trichocephalus dispar in the cæcum. One kind of Distoma has its place in the lungs of the green frog, another in those of the brown frog. Cysticercus cellulosæ is found in the connective tissue; Trichina spiralis in the substance of the muscles.

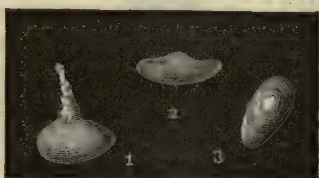
With regard to many of these parasites the only difficulty in accounting for their existence, except on the presumption of their spontaneous generation, lay in their being confined to such narrow limits and their never being met with elsewhere. It seemed probable that some local combination of conditions was necessary to the production of a parasite, which was never to be found except in the biliary passages, the kidneys, or the lungs of a living animal. A little consideration, however, makes it evident that these conditions are in reality neither necessary nor sufficient for the production, but only for the *development* of the parasites in question. Most of the internal parasites evidently reproduce their species by generation. They have male and female organs, and produce fertile eggs, often in great abundance. The eggs contained in a single female Ascaris are to be counted by thousands; and in a tapeworm even by millions. These eggs, in order that they may be hatched, and produce new individuals, require certain special

conditions which are favorable for their development; in the same manner as the seeds of plants require, for their germination and growth, a certain kind of soil and a certain supply of warmth and moisture. It is accordingly no more remarkable that Oxyuris vermicularis should inhabit the rectum, and Ascaris lumbricoides the ileum, than that Lobelia inflata should grow only in dry pastures, and Lobelia cardinalis by the side of running brooks. The lichens flourish on the exposed surfaces of rocks and stone walls; while the fungi vegetate in darkness and moisture, on the decaying trunks of dead trees. Yet both these classes of vegetables are well known to be reproduced by generation, from germs which require special conditions for their growth and development. If the germ of any species, whether animal or vegetable, be deposited in a locality where these requisite conditions are present, it is developed and comes to maturity; otherwise not. This accounts fully for the fact that internal parasites, like other living organisms, are confined to certain situations by the requirements of their nourishment and growth.

But in regard to a few of the internal parasites a further difficulty existed, owing to the presence of two peculiaries: first, these particular kinds do not inhabit the open passages or canals of the body, but lie encysted, in the solid substance of the tissues, where there are no visible means of access from without; and secondly, they are sexless, performing no generative function, and having no progeny of their own; so that it does not readily appear how they can themselves have been derived from parents. The two kinds of entozoa which have presented this difficulty in the most marked manner, and in which it has been most fully explained by the results of observation and experiment, are those known as Cysticercus cellulosæ and Trichina spiralis.

1. *Cysticercus cellulosæ.*—This is a bladder-shaped parasite of somewhat flattened form, about 10 millimetres in diameter, found in the subcutaneous and intermuscular connective tissue of the pig, where it appears under the form of whitish specks, giving to the flesh the appearance known as that of "measly pork." Each parasite is enveloped in a perfectly closed cyst, but the bladder-like body, when extracted, exhibits at one spot a minute depression or involution of its wall. From this point a slender neck, ending in a rounded head, may be extruded by pressure; after which the animal is seen to consist of a head and neck, terminated posteriorly by a dilated, sac-like tail, whence its generic name of cysticercus. Its specific name was derived from its inhabiting the connective tissue, formerly known as the "cellular tissue." The head of the parasite, when magnified, shows upon its surface four sucking disks,

Fig. 214.



CYSTICERCUS CELLULOSÆ, from the flesh of the pig. Natural size.—1. Vesicular appendage, with the head and neck extruded. 2, 3. The same, with head and neck inverted; viewed in different positions. (Davaine.)

and near its extremity a double crown of curved calcareous processes or hooks, implanted in its substance. There are no distinguishable internal organs, and the caudal vesicle is filled simply with an albuminous watery fluid. Thus there is no apparent source from which these organisms can have come, other than the tissues which they inhabit, nor any visible mode of continuing the species by generation.

But it has been shown by the investigations of Van Beneden, Leuckart, Haubner, and Küchenmeister,[1] that Cysticercus cellulosæ is only the embryonic progeny of Tænia solium, or the solitary tapeworm, found in the small intestine of the human subject. The specific identity of the two was first suspected from the exact similarity in the form and structure of the head and narrow neck, which presents the same sucking disks and double crown of hooks in Tænia as in Cysticercus. But in Tænia this neck, instead of terminating in a vesicular appendage, is elongated and transversely wrinkled. The wrinkles, after a certain distance, become deepened into superficial furrows, marking off the body of the animal into oblong divisions or articulations, each articulation showing a double system of communicating vascular canals, and also distinctly marked generative organs of both sexes. As they recede, by successive growth, farther and farther from the head, the generative organs contained in the articulations become more completely formed, and are at last filled with mature fecundated eggs, in which the embryos have begun to be developed. The entire tapeworm then forms a continuous chain or colony of articulations, sometimes from six to eight metres in length, and attached to the mucous membrane of the intestine only by the minute head at its anterior extremity.

Fig. 215.

TÆNIA SOLIUM.

By the experiments above mentioned it was found, 1st. That mature articulations from the tænia solium of the human subject, if administered to young pigs with their food, produce an abundance of cysticercus cellulosæ in the flesh of these animals; and, 2d. That cysticercus cellulosæ from measly pork, if swallowed by man, becomes developed in the intestine within a few days, into ribbon-like worms, distinctly recognizable as young specimens of tænia solium.

The manner in which the pig becomes infested with cysticercus is as follows: In the fully-formed tapeworm, in the human intestine, the last

[1] Küchenmeister, Animal and Vegetable Parasites. Sydenham edition, London, 1857, pp. 115, 120.

and most mature articulations separate spontaneously from the rest of the colony, and either find their way out by the anus singly, or are discharged with the evacuations. They have, while still living, a considerable degree of contractility and power of locomotion; and thus become accidentally transferred to the surface of neighboring vegetable matters, and are devoured by the pig with his food. In the stomach and intestine, the substance of the articulation is digested and dissolved; but the embryos, which are 33 mmm. in diameter, and armed with three pairs of calcareous spines, make their way through the intestinal walls, and thence are dispersed, either by a continuance of the same movement or by the bloodvessels, throughout the connective tissue, where they are afterward found. Here they become encysted, and go through with a partial development, remaining in the condition of cysticercus in the flesh of the pig until this flesh is used for food, when they finally become converted into tænia solium. Thus the entire round of generation and development is completed, and the original form of the parasite reproduced. A similar relation has been shown by Küchenmeister and Siebold[1] to exist between certain other species of tænia and cysticercus.

2. *Trichina spiralis.*—This is a sexless, encysted, worm-like parasite, found in the muscular tissue of the pig, and sometimes in that of the rat, the cat, and the human species. Each worm lies closely coiled, in a spiral form, in the interior of its enveloping cyst. It is about 0.75 millimetre in length, of a tapering form, with a slender anterior and rounded posterior extremity. It presents a nearly straight intestine extending through its whole length, and rudimentary sexual organs which are entirely inactive. The worm has been known since 1835, as occasionally found in the human muscular tissue in the encysted form; but it is only since 1860, principally from the investigations of Leuckart,[2] that the different stages of its growth and development have been made known. If muscular flesh containing encysted trichinæ be administered with the food to a rabbit, cat, rat, mouse, or pig, the cysts become digested and the worms liberated in the small intestine. Here they rapidly increase in size and development, the females becoming impregnated and filled with living young, and attaining, at the end of a fortnight, three or four times their previous size. The young embryos are now discharged from the body of the parent, make their way through the walls of the intestine, and are

Fig. 216.

TRICHINA SPIRALIS, encysted, from muscular tissue of a trichinous cat. Magnified 76 diameters.

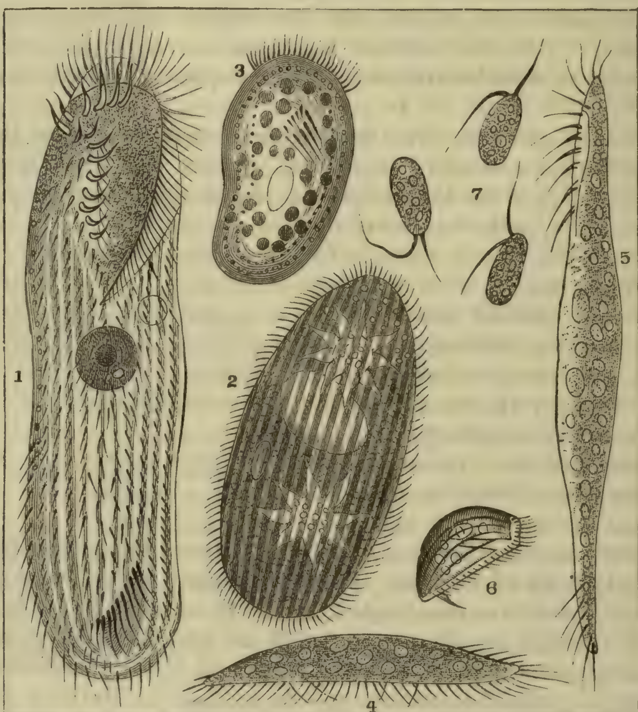
[1] Von Siebold, On Tape and Cystic Worms. Sydenham edition. London, 1857, p. 57.

[2] Untersuchungen über Trichina spiralis. Leipzig und Heidelberg, 1860.

dispersed throughout the body. They thus reach the muscular tissue, where they become encysted, and remain quiescent until again introduced into the intestine of another animal or of man. In this way the existence of sexless and encysted parasites is seen to be entirely analogous to that of the caterpillar or the maggot. They are sexless, because they are still in the embryonic or incomplete stage of development. But they have been produced by the regular mode of generation from parents; and they will, at a subsequent period, themselves produce young by the same process.

II. *Infusoria.*—These are microscopic organisms, first discovered by Leeuwenhoek, in 1675, in rain-water which had been kept in standing vases. On account of their active movement and minute size he called them "animalcules;" but as they were soon afterward discovered to

Fig. 217.



INFUSORIA, of various kinds.—1. Urostyla grandis, from decaying sedge-grass 2. Paramecium aurelia, from vegetable infusions. 3. Chlamydodon mnemosyne, Baltic Sea water. 4. Kerona polyporum, on the fresh-water polype. 5. Oxytricha caudata, open stagnant waters. 6. Ervilia fluviatilis, clear brook water. 7. Heteromita ovata, on aquatic river-plants. Magnified 325 diameters. (Ehrenberg and Stein.)

make their appearance in great numbers and with remarkable rapidity in watery infusions of organic matter exposed to the air, they received the general name of "infusoria." They present themselves in great variety, and under rapidly changing forms; so much so that Ehrenberg

in 1838[1] described more than 700 different kinds. They are generally provided with cilia attached to the exterior of their bodies, and are, for the most part, in constant and rapid motion in the fluid which they inhabit.

In consequence of the numerous different forms of the infusoria, their frequent changeability of figure, and their want of resemblance to any previously known class of animal organisms, they were thought, by some of the earlier observers, to have no regular mode of generation, but to arise indiscriminately from the organic materials of the infusion; the particular form which they might assume being determined by the special conditions of each case. Their inevitable appearance in organic infusions, at all ordinary temperatures and exposures, contributed to sustain this belief. The substance of the infusion might be previously baked or boiled; the water in which it was infused might be distilled, and thus freed from all organic contamination; and yet the infusoria would make their appearance at the usual time and in the usual abundance, provided only that the infusion were exposed to moderate warmth and to the access of atmospheric air. But these conditions are essential to maintaining the life of all organized creatures, from whatever source they may come, and are not, therefore, more necessary to the infusoria than to others.

Therefore the infusoria must either have been spontaneously generated from the materials of the infusion, or else they must have been produced from germs introduced from the atmosphere. In the latter case these germs must be wafted about, in a comparatively dry state and in an inactive condition, by the atmospheric currents, to resume their activity and development when brought in contact with sufficient moisture and with the organic material requisite for their nutrition.

The researches relating to this question continued with the most extraordinary persistence, and with various interruptions and revivals, from 1775, when they were carried on by Needham and Spallanzani, throughout the greater part of the present century, in the hands of Cuvier, Schultze, Helmholtz, Milne-Edwards, Longet, Pouchet, Pasteur, Wyman, and Bastian. The main object of investigation was to discover whether, if all previous living germs were destroyed by heat, and the access of others prevented by hermetically sealing the vessels, or thoroughly purifying the air which was introduced, infusorial life would, under such circumstances, be developed.

The general result of these experiments was that such precautions diminished and often entirely prevented the production of infusoria. Spallanzani[2] had already shown in 1776 that organic infusions in hermetically sealed glass flasks, if boiled for two minutes, failed to produce any of the larger and more highly organized animalcules; and that boiling for three-quarters of an hour prevented the appearance of the more minute and simpler kinds.

[1] Die Infusionsthierchen als vollkommene Organismen. Leipzig, 1838.

[2] Opuscoli de Fisica animale e vegetabile. Modena, 1776, vol. i. p. 10.

Schultze[1] performed similar experiments, with the additional advantage of admitting to the organic infusion fresh air purified from germs. He placed his infusion in a glass flask, the stopper of which was provided with two narrow tubes, bent at right angles. When the infusion had been thoroughly boiled, and all the air contained in the flask expelled, he fastened to each of the projecting tubes a series of bulbs containing on the one side sulphuric acid, and on the other a solution of potassium hydrate; so that the air which re-entered the flask while it was cooling must pass through these fluids, and thus be cleansed of all living organic matter. The apparatus was then kept in a warm place for two months, the air being renewed daily by suction through the tubes, without any infusoria being detected in its contents. But they showed themselves in great abundance after it had been taken apart, and the infusion exposed for a few days directly to the atmosphere.

Pasteur[2] found that if a flask containing an organic liquid were boiled upon a high mountain, where the air is of unusual purity, allowed to fill itself with this air while cooling, and then hermetically sealed, it would often remain free from infusorial growth. He kept several such flasks, boiled and filled with air upon the Montanvert in Switzerland, for four years, without the liquids which they contained undergoing any perceptible change. But on making, at the end of that time, a minute opening in the neck of one of these flasks, it exhibited after three days a perceptible growth of cryptogamic vegetation.

These results did not absolutely exclude the possibility of spontaneous generation, which was still maintained by Pouchet and a number of other observers; but they indicated in a very decisive manner that the atmosphere might contain the inactive germs of infusoria, which were capable of being developed on meeting with a suitable organic infusion.

But in the mean time the study of the infusoria themselves had been going on independently of the question of spontaneous generation, and this alone has been sufficient to demonstrate that they are reproduced in the usual way, like other animal species, by means of fertilized eggs and embryonic development.

The apparent confusion and variability in form of the infusoria, at the time of their first discovery, depended only upon their great numbers and upon the want of sufficient knowledge in regard to them. Subsequent observation has shown that their organization is as definite as that of other classes of the animal kingdom; and they have now been arranged, by the labors of Claparède and Lachmann,[3] Stein,[4] and Balbiani,[5] into orders, families, genera, and species, which may be recog-

[1] Poggendorf's Annalen, 1836. Band xxxix. p. 487.

[2] Comptes Rendus de l'Académie des Sciences. Paris, Février 20, 1865.

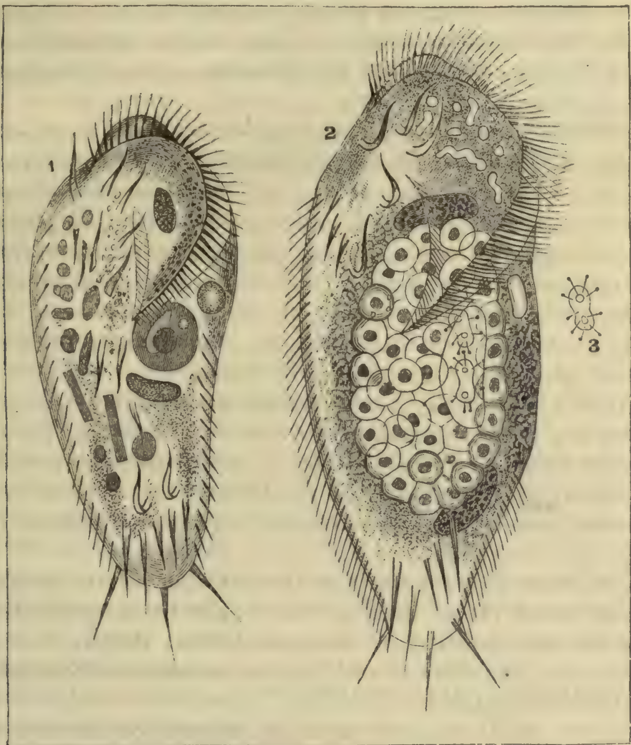
[3] Etudes sur les Infusoires et les Rhizopodes. Genève, 1856–1861.

[4] Organismus der Infusionsthiere. Leipzig, 1859.

[5] Journal de la Physiologie de l'Homme et des Animaux. Paris, 1861.

nized with certainty by their distinctive marks. They are not confined to infusions of decaying material artificially or accidentally prepared; but many of them have their natural habitation in the clearest waters of lakes, pools, marshes, running brooks, or the open sea. Certain forms, originally included in this class, such as Rotifer, Stephanoceros, and Floscularia, have been found to possess a more complicated structure than the rest, and to belong properly to the class of worms; while their mode of reproduction is sufficiently manifest from the fact that living embryos, in process of development, are often to be seen in their interior.

Fig. 218.



STYLONYCHIA MYTILUS; a fresh-water infusorium.—1. Unimpregnated. 2. Impregnated, and containing mature eggs and two embryos. 3. Showing the form of the embryo. Magnified 375 diameters. (Stein.)

Finally, the ciliated infusoria themselves have been shown to reproduce their species by means of eggs, formed in special generative organs and fecundated by union of the sexes (Fig. 218). This fact, first demonstrated by Balbiani, has been since confirmed, in many instances, by Stein, Engelmann,[1] and Cohn;[2] Balbiani and Stein together having

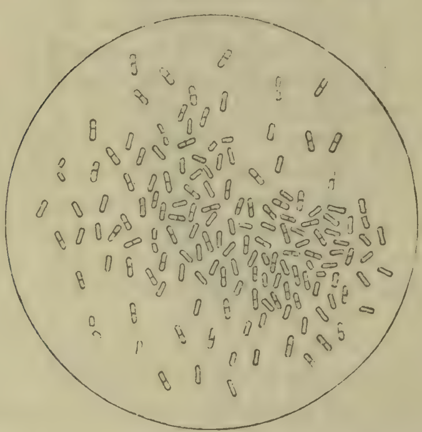
[1] Zeitschrift fur Wissenschaftliche Zoologie. Leipzig, 1862, Band xi. p. 347.
[2] Ditto. Band xii. p. 197.

observed the occurrence of sexual generation in 47 different genera and 66 different species.

Thus the infusoria proper are in their turn excluded from the field of spontaneous generation. But, on the other hand, a considerable group of organisms, formerly referred to the class of infusoria, are now known to be of a different character. These are the forms included under the general term of *Bacteria*, and comprising the special varieties of bacterium, vibrio, spirillum, and micrococcus. They are demonstrated to be of a vegetable nature, notwithstanding their frequent exhibition of rapid and continuous movement; and they consist of cells, which multiply, often in great abundance, by a process of repeated subdivision. Whether they are also reproduced by means of spores or germs, has not been determined; but their minute size and their imperfect classification have thus far proved obstacles to the complete study of their physiological characters.

The representative of this group may be considered to be the species known as *Bacterium termo*, already described (page 83), in connection with the phenomena of putrefaction. It consists of elongated or rod-like cells, averaging 3 mmm. in length by 0.6 mmm. in thickness, sometimes single, often double, two of them being attached, more or less firmly, end to end. The latter appearance is due to the progressive multiplication of the cells, which takes place by a transverse division at the middle of their length. The two new cells thus produced remain for a time in connection with each other, and afterward separate, to repeat the process independently of each other. The final separation of two cells may often be seen to occur under the microscope. The bacterium cells, during a considerable part of their existence, are in rapid vibratory and progressive movement. The vibrations take place in a circular manner, about some point situated either at or near one of the extremities; so that the rest of the cell performs a conical movement around this point, presenting, on superficial examination, the appearance of a lateral oscillation. The mechanism by which this vibration is accomplished is unknown; but it is no doubt analogous to the slower spiral undulations of the *Oscillatoriæ*, among fresh-water algæ; and its effect is to propel the

Fig. 219.



Cells of BACTERIUM TERMO; from a putrefying infusion.

bacterium cells, often with extreme velocity, through the fluid in which they are immersed.

Of later years, the investigations in regard to spontaneous generation have been almost exclusively confined to the bacteria and their allies, since they now form the only group of organisms in which reproduction by generation has not been fully established. Even for them, the rapid multiplication by cell division, which takes place under favorable conditions, indicates the usual mode of their increase in numbers; but in order to establish an entire similarity between them and other living organisms, they must also be shown to reproduce themselves by spores or germs, which has not thus far been done. The experiments with boiled infusions in sealed flasks have led to results which are not interpreted in the same manner by all writers; but it is evident that for bacteria, as well as for other organic forms, the application of heat exerts in various degrees a preventive action on their subsequent appearance.

Among the most careful and satisfactory experiments on this part of the subject are those of Prof. Wyman,[1] who operated with infusions of both animal and vegetable matters. The infusions, placed in sealed flasks, with abundance of atmospheric air, were submerged in boiling water for periods varying from thirty minutes to five hours, and afterward kept under observation at the ordinary temperatures requisite for the development of bacteria. The result showed that the appearance of these organisms was always delayed by the previous application of heat, and that this delay, in different series of observations, was often in direct proportion to the length of time during which the boiling had been continued. Furthermore, in certain cases the bacteria failed to be produced at all, and the chances of their production decreased in proportion to the length of time during which the liquid had been boiled. Thus, of four series of flasks, each containing the same infusion, and boiled respectively during one, two, three, and four hours, all of the first and second series afterward produced bacteria, only one of the third, and none of the fourth. Finally, in no instance, among numerous trials, did they appear in any infusion which had been boiled for a period exceeding five hours. Thus a limit was reached to the production of bacteria, in fluids previously subjected to the action of heat.

There can be no doubt as to the scientific bearing of these and similar experiments. Spontaneous generation is inadmissible at the present day for everything except bacteria; and with regard to them there is no sufficient proof that they are ever generated without the concurrence of previously existing germs.

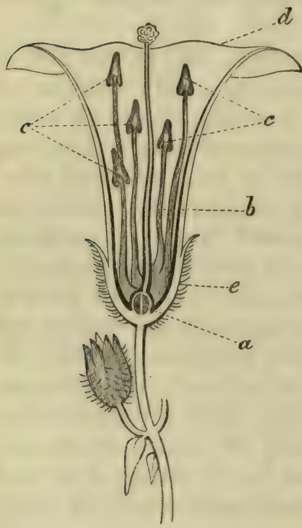
[1] American Journal of Science and Arts. New Haven, vol. xliv., September, 1867.

CHAPTER II.

SEXUAL GENERATION, AND THE MODE OF ITS ACCOMPLISHMENT.

Sexual generation is performed by two sets of organs, each of which gives origin to a peculiar product, capable of uniting with the other, to produce a new individual. These organs, belonging to the two different sexes, are called the male and female organs of generation. The female organs produce a globular body called the *egg* or *germ*, which is capable of being developed into the body of the young animal or plant; the male organs produce a substance which is necessary to fecundate the germ, and enable it to go through with the process of growth and development.

Fig. 220.



Blossom of Ipomœa Purpurea. (Morning-glory.)—*a.* Germ. *b.* Pistil. *c. c.* Stamens, with anthers. *d.* Corolla. *e.* Calyx.

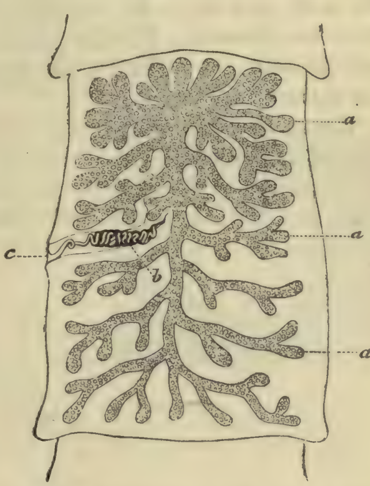
Such are the essential and universal characters of the organs of generation. These organs, however, while exhibiting everywhere the same principal features, present certain modifications of structure and arrangement in different classes of organized beings.

In the flowering plants, the blossom, which is the generative apparatus (Fig. 220), consists first of a female organ containing the germ (*a*), situated usually upon the highest part of the leaf-bearing stalk. This is surmounted by a nearly straight column, termed the pistil (*b*), dilated at its summit into a globular expansion, and occupying the centre of the flower. Around it are arranged several slender filaments, or stamens, bearing upon their extremities the male organs, or anthers (*c*, *c*). The whole is surrounded by a circle or crown of delicate colored leaves, termed the corolla (*d*), which is frequently provided with a smaller sheath of green leaves outside, called the calyx (*e*). The anthers, when arrived at maturity, discharge a fine organic dust, called the pollen, the grains of which are caught upon the extremity of the pistil. Each pollen-grain then absorbs the nutritious juices with which it is in contact, and develops from its substance a tubular prolongation, the pollen-tube, which, by its con-

tinued growth, penetrates downward through the tissues of the pistil until it comes in contact with the germ below. The germ thus fecundated, the process of generation is accomplished. The pistil, anthers, and corolla wither and fall off, while the germ increases in size, and changes in form and texture, until it ripens into the mature fruit or seed. It is then ready to be separated from the parent stem; and, if placed in the proper soil, will germinate and produce a new plant similar to the old.

In many species of plants, the male and female organs, as above described, are both situated upon the same flower; as in the lily, the violet, the convolvulus. In other instances, there are separate male and female flowers upon the same plant, of which the male flowers produce only the pollen, the female, the germ and fruit. In others still, the male and female flowers are situated upon different plants, which otherwise resemble each other, as in the willow, the poplar, the sassafras.

Fig. 221.



SINGLE ARTICULATION OF TÆNIA CRASSICOLLIS, from the cat.—*a, a, a.* Ovary filled with eggs. *b.* Testicle. *c.* Genital orifice.

In animals, the female organs of generation are called *ovaries*, since it is in them that the egg, or "ovum," is produced. The male organs are the *testicles*, which give origin to the fecundating product, the "sperm" or "seminal fluid," by which the egg is fertilized. In the tænia or tapeworm, already described (page 674), each articulation contains both ovary and testicle. The ovary (Fig. 221, *a*, *a*, *a*) is a series of branching tubes ending in rounded follicles, and communicating with a central canal. The testicle (*b*) is a narrower convoluted tube, closely folded upon itself, and opening by an external orifice (*c*) upon the lateral border of the articulation. The seminal fluid produced in the testicle is introduced into the female generative passage, which opens at the same spot, and, penetrating into the interior, comes in contact with the eggs, which are thereby fecundated. Each egg then produces a young embryo, which is capable of being afterward developed into a full-grown tænia.

In various other families of invertebrate animals, as the snail, the slug, the leech and the earth worm, an ovary and a testicle are both present in the body of the same individual. But in these instances impregnation is effected only by the concurrent action of two different organisms; and when sexual union takes place, the eggs produced by

one animal are fecundated by the seminal fluid of another, and *vice versâ.*

In all the vertebrate animals, on the other hand, the two sets of generative organs are located in separate individuals; and the species is divided into two sexes, male and female. Beside this, there are, in most instances, certain secondary or accessory organs of generation, which assist in the accomplishment of the process, and which occasion a correspònding difference in the anatomy of the two sexes. In some cases this difference is so great that the male and female would never be recognized as belonging to the same species, unless they were seen in company with each other, and were known to reproduce the species by sexual congress. Not to mention some extreme instances of this among insects and other invertebrate animals, it is sufficient to refer to the well-known examples of the cock and the hen, the lion and lioness, the buck and the doe. In the human species, the distinction between the sexes shows itself in the mental constitution, the disposition, habits, and pursuits, as well as in the general conformation of the body, and the external appearance.

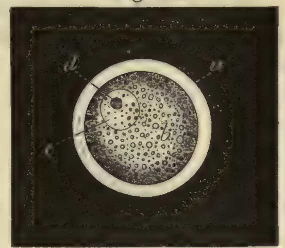
The special details of the generative process depend upon the structure of the male and female organs, the manner in which their products are formed and discharged, the union of the two in the act of fecundation, and the changes which take place in the development of the embryo.

CHAPTER III.

THE EGG, AND THE FEMALE ORGANS OF GENERATION.

The egg, in man and in all species of mammalians, presents an essential similarity of form, size, and structure. It is a globular body, about 0.25 millimetre in diameter, and consists of two parts, namely, first, an external closed sac, the *vitelline membrane;* and, secondly, a spherical mass contained in its interior, the *vitellus*. Of these two, the vitellus is the essential constituent part of the egg, since it is from its substance that the rudiments of the embryo are formed. The vitelline membrane is a protective envelope, destined to maintain the form and integrity of the vitellus.

Fig. 222.



Human Ovum, magnified 75 diameters.—*a.* Vitelline membrane. *b.* Vitellus. *c.* Germinative vesicle. *d.* Germinative spot.

Vitelline Membrane.—The vitelline membrane is a smooth, transparent, colorless layer, about .01 millimetre in thickness. When viewed with magnifying powers sufficiently moderate to include the view of the whole egg, the membrane presents a perfectly homogeneous aspect; although with higher powers, according to Klein, it exhibits an appearance of vertical striations. Notwithstanding its delicacy and transparency, it is very elastic, and has a considerable degree of retistance. If the egg of the human species, or of any of the mammalians, be placed under the microscope, surrounded by fluid and covered with a thin slip of glass, it may be perceptibly flattened out by pressing upon the cover-glass with the point of a steel needle; and when the pressure is removed it readily resumes its globular form. When the egg is partially flattened in this way, by the pressure of a needle or by the weight of the cover-glass, the apparent thickness of the vitelline membrane is increased, giving it the appearance of a rather wide, pellucid border or zone, surrounding the granular and comparatively opaque vitellus. From this circumstance it has sometimes received the name of the "zona pellucida."

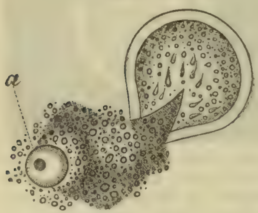
In the vitelline membrane of many invertebrates, and also in that of fishes, a minute opening has been discovered, termed the "micropyle," leading into the interior of the vitelline cavity; and it is through this opening that the filaments of the male seminal fluid penetrate, to reach the vitellus. It is very possible that such an opening may also exist

in the vitelline membrane of man and the other vertebrate animals; but the globular form of the egg, the transparent and homogeneous texture of the vitelline membrane, and the absence of any other material, of different refractive power, in the canal or orifice of the micropyle itself, prevent its being detected in microscopic examination.

Vitellus.—The vitellus is a globular mass, of semifluid, tenacious consistency, composed of a transparent and colorless albuminous material, with oleaginous looking granules thickly disseminated throughout its substance. Owing to the physical admixture of these two constituents, it has a distinctly granular aspect, and a considerable degree of opacity. Imbedded in the vitellus, at a point near its surface, and consequently almost immediately beneath the vitelline membrane, is a clear, colorless, transparent vesicle, of a rounded form, the *germinative vesicle*. In the mammalian egg, this vesicle measures about .04 millimetre in diameter. It presents upon its surface a nucleus-like spot, known by the name of the *germinative spot*. Both the germinative vesicle and germinate spot are partially concealed, in the uninjured condition of the egg, by the granules of the surrounding vitellus.

If the egg, while under the microscope, be ruptured by continued pressure upon the covering glass, the semifluid vitellus is gradually expelled by the elasticity of the vitelline membrane. It retains the granules imbedded in its substance, but often allows the germinative vesicle to become detached, and therefore more distinctly visible.

Fig. 223.



Human Ovum, ruptured by pressure, showing the vitellus partially expelled, the germinative vesicle, with its germinative spot, at *a* and the smooth fracture of the vitelline membrane.

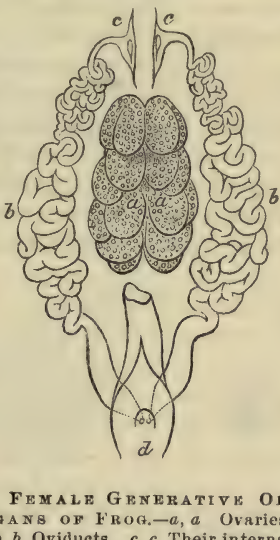
In man and the mammalians, the simple form of egg above described, consisting mainly of a vitellus of minute size, is sufficient for the production of the embryo, since it is retained, after fecundation, in the interior of the generative passages, and absorbs the nutritious materials for its subsequent growth from the tissues of the female parent. In the naked reptiles and in most fish, where the eggs are deposited and hatched in the water, the vitellus is also of small size; since the hatching takes place at a comparatively early period of development, and the requisite additional fluid is supplied from the surrounding medium. But in birds, and in most of the scaly reptiles, as serpents, turtles, and lizards, the eggs are deposited in a nest or in the ground, and there is consequently no external source of nutrition for the support and growth of the embryo during its development. In these instances the vitellus, or "yolk," is of large size; and the bulk of the egg is still further increased by the addition, within the female generative passages, of layers of albumen and various external fibrous and calcareous envelopes. The essential constituents of the egg, nevertheless, still remain the same in character, and the process of embryonic development follows its usual course.

Ovaries and Oviducts.—The eggs are produced in the interior of certain organs, situated in the abdominal cavity, called the *ovaries.* These organs consist of a mass of vascular connective tissue, inclosing a number of globular sacs or follicles, the "Graafian follicles;" so called from the name of the anatomist who first fully described them[1] as constituent parts of the ovary. Each Graafian follicle contains an egg, which varies more or less in size and appearance in different classes of animals, but which has always the same essential characters, and is produced in the same way.

The egg thus grows in the interior of the ovarian sac, like a tooth in its follicle; and forms, accordingly, a constituent part of the body of the female. It is destined to be subsequently separated from its attachments, and thrown off; but until that time, it is one of the elements of the tissue of the ovary, and is nourished like any other portion of the female organism.

Since the ovaries are the organs directly concerned in the production of the egg, they form the most essential part of the female generative apparatus. Beside them, there are usually present certain other organs, which play a secondary part in the process of generation. The most important of these accessory organs are two symmetrical tubes, or *oviducts*, destined to receive the eggs at their inner extremity and convey them to the external generative orifice. The mucous membrane lining the oviducts is also adapted by its structure to supply certain secretions during the passage of the egg, which are requisite, either to complete its formation, or to provide for the nutrition of the embryo.

Fig. 224.



Female Generative Organs of Frog.—*a, a* Ovaries. *b, b.* Oviducts. *c, c.* Their internal orifices. *d.* Cloaca, showing inferior orifices of oviducts.

In the frog, the oviduct commences at the upper part of the abdomen, by a rather wide orifice, communicating directly with the peritoneal cavity. It soon afterward contracts to a narrow tube, and pursues a zigzag course down the side of the abdomen (Fig. 224), folded upon itself in numerous convolutions, until it opens, near its fellow of the opposite side, into the "cloaca" or lower part of the intestinal canal. The oviducts present the general characters described above in nearly all species of reptiles and birds.

The ovaries, as well as the eggs which they contain, undergo at particular seasons a periodical development or increase in growth. In the female frog, during the latter part of summer or the fall, the ova-

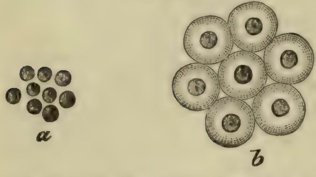
[1] Regner de Graaf, Opera Omnia. Amstelædami, 1705, p. 228.

ries appear like small clusters of minute and nearly colorless eggs, the smaller of which are perfectly transparent and less than 0.18 millimetre in diameter. But in the early spring, when the season of reproduction approaches, the ovaries increase to four or five times their former size, forming large lobulated masses, crowded with dark-colored opaque eggs, each 2 millimetres in diameter. At the generative season, in all the lower animals, a certain number of eggs, which were previously in an imperfect condition, increase in size and become altered in structure. The vitellus especially, which was before colorless and transparent, becomes granular and increased in volume; and it assumes at the same time a black, brown, yellow, or orange color. In the mammalian egg the change consists only in an increase of size and granulation, without any remarkable alteration of color.

The eggs, as they ripen in this way, gradually distend the Graafian follicles and project from the surface of the ovary. When fully ripe, they are discharged by a rupture of the follicles, and, passing into the oviducts, are conveyed to the external generative orifice, and there expelled. In successive seasons, successive crops of eggs enlarge, ripen, leave the ovaries, and are discharged. Those which are to be expelled at the next generative epoch may be recognized by their greater degree of development; and in this way, in many animals, the eggs of no less than three different crops may be distinguished in the ovary at once, namely, 1st, those which are perfectly mature and ready to be discharged; 2d, those which are to ripen in the following season; and 3d, those which are as yet inactive and undeveloped. In most fish and reptiles, as well as in birds, this regular process of the ripening and discharge of eggs takes place but once a year. In different species of quadrupeds it may occur annually, semi-annually, bi-monthly, or even monthly; but in every instance it returns at regular intervals, and exhibits, therefore, a well-marked periodical character.

Action of the Oviducts and Female Generative Passages.—In the frog, after the ripening of the eggs and their discharge from the ovarian follicles, they receive an additional investment while passing through the oviducts. At the time of leaving the ovary, the eggs consist simply of the dark-colored and granular vitellus, inclosed in the vitelline membrane. They are received by the inner extremity of the oviducts, and carried downward by the peristaltic movement of these canals, aided by the contraction of the abdominal muscles. During their passage, the mucous membrane of the oviduct secretes an albuminous substance, which is deposited in successive layers, forming round each egg a thick coating or envelope (Fig. 225). When the eggs are discharged, this envelope absorbs moisture from the water in which the spawn is deposited, and

Fig. 225.



MATURE FROGS' EGGS.—*a.* While still in the ovary. *b.* After passing through the oviduct.

swells into a transparent gelatinous mass, in which the eggs are separately imbedded. It supplies, by its subsequent liquefaction and absorption, a certain amount of nutritious material, for the development and growth of the embryo.

In the scaly reptiles and in birds, the oviducts perform a more important function. In the common fowl, the ovary consists, as in the frog, of follicles, loosely united by connective tissue, and containing eggs in different stages of development (Fig. 226, *a*). As the egg which is approaching maturity enlarges, it distends the cavity of its follicle, and projects farther from the general surface of the ovary; so that it hangs at last into the peritoneal cavity, retained only by the attenuated wall of the follicle, and a slender pedicle through which run the bloodvessels by which its circulation is supplied. A rupture of the follicle then occurs at its most prominent part, and the egg is discharged from the lacerated opening.

At the time of leaving the ovary, the egg of the fowl consists of a large, globular, orange-colored vitellus, or "yolk," inclosed in a thin and transparent vitelline membrane. Immediately underneath the vitelline membrane, at one point upon the surface of the vitellus, is a round white spot, consisting of a layer of minute granules, termed the "cicatricula," in which the germinative vesicle is imbedded at an early stage of the development of the egg. At the time of its discharge from the ovary, the germinative vesicle has usually disappeared; but the cicatricula is still an important part of the vitellus, and it is from this spot that the body of the chick begins afterward to be developed.

As the egg protrudes from the surface of the ovary, it projects into the inner orifice of the oviduct; so that, when discharged from its follicle, it is embraced by the upper expanded extremity of this tube, and commences its passage downward. In the fowl, the muscular coat of the oviduct is highly developed, and its peristaltic contractions urge the egg from above downward, somewhat in the same manner as the œsophagus or the intestines transport the food in a similar direction. While passing through the first five or six centimetres of the oviduct (*c*, *d*), where the mucous membrane is smooth and transparent, the yolk absorbs a certain quantity of fluid, becoming consequently rather more flexible and yielding in consistency. It then passes into a second division of the generative canal, in which the mucous membrane is thicker and more glandular, and is thrown into longitudinal folds. This portion of the oviduct (*d*, *e*) extends over about 22 centimetres, or more than one-half its entire length. In its upper part, the mucous membrane secretes a viscid material, by which the yolk is incased, and which soon consolidates into a gelatinous deposit, thus forming a second envelope, outside the vitelline membrane.

The peristaltic movements of this part of the oviduct are such as to give a rotary, as well as a progressive motion to the egg; and by this means the two extremities of the gelatinous envelope become twisted in opposite directions; forming two whitish looking cords, attached

to the opposite poles of the egg. These cords are termed the "chalazæ," and the membrane with which they are connected, the "chalaziferous membrane."

Throughout the remainder of the second division of the oviduct, the mucous membrane exudes an albuminous substance, which is deposited in successive layers round the yolk, inclosing the chalaziferous membrane and the chalazæ. This substance, the so-called albumen, or "white of egg," is gelatinous in consistency, nearly transparent, and of a faint amber color. It is deposited in greater abundance in front of the advancing egg than behind it, and thus forms a conical projection anteriorly, while behind, its outline is parallel with the spherical surface of the yolk. In this way, the egg acquires, when covered with its albumen, an ovoid form, of which one end is round, the other pointed; the pointed extremity being directed downward, as the egg descends along the oviduct.

In the third division of the oviduct (*f*), which is about nine centimetres in length, the mucous membrane is arranged in longitudinal folds, which are narrower and more closely packed than in the preceding portion. The material secreted in this part condenses into a firm fibrous covering, composed of three different layers which closely embrace the surface of the albuminous mass, forming a tough, flexible, semi-opaque envelope for the whole. These layers are known as the external, middle, and internal fibrous membranes of the egg.

Finally the egg passes into the fourth division of the oviduct (*g*), which is wider than the rest of the canal, but only a little over five centimetres in length. Here the mucous membrane, which is arranged in abundant projecting, leaflike villosities, exudes a fluid rich in

Fig. 226.

Female Generative Organs of the Fowl.—*a.* Ovary. *b.* Graafian follicle, from which the egg has just been discharged. *c.* Yolk, entering upper extremity of oviduct. *d, e.* Second division of oviduct, in which the chalaziferous membrane, chalazæ, and albumen are formed. *f.* Third portion, in which the fibrous shell membranes are produced. *g.* Fourth portion laid open, showing the egg completely formed, with its calcareous shell. *h.* Narrow canal through which the egg is discharged.

calcareous salts. The most external of the three membranes above described is permeated by this secretion; and soon afterward, owing to the reabsorption of its fluid parts, the calcareous matter begins to crystallize in the fibrous network of the membrane. This deposit of calcareous matter goes on, growing thicker and more condensed, until the external envelope is converted into a white, opaque, brittle, calcareous shell, which incloses the remaining portions and protects them from injury. The egg is then forced through a narrow portion of the oviduct (*h*), and, gradually dilating the passages by its conical extremity, is finally discharged from the external orifice.

The egg of the fowl, after its expulsion, consists, accordingly, of various parts; some of which, as the yolk and the vitelline membrane, entered into its original formation, while the remainder have been deposited round it during its passage through the oviduct.

After the discharge of the egg there is a partial evaporation of its watery ingredients, which are replaced by air penetrating through the pores of the shell at its rounded extremity. The air thus introduced accumulates between the middle and internal fibrous membranes, forming a cavity or air-chamber (*g*), at the rounded end of the egg. Very

Fig. 227.

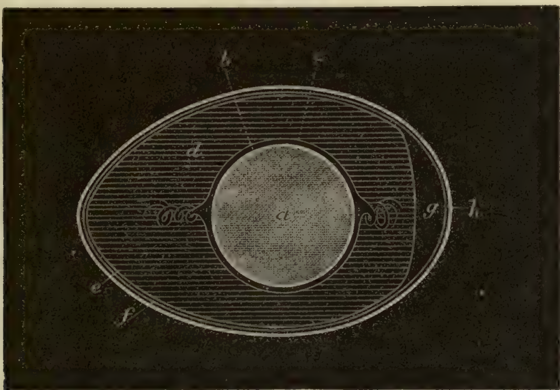


Diagram of FOWL'S EGG.—*a.* Yolk. *b.* Vitelline membrane. *c.* Chalaziferous membrane. *d.* Albumen. *e, f.* Middle and internal shell membranes. *g.* Air-chamber. *h.* Calcareous shell.

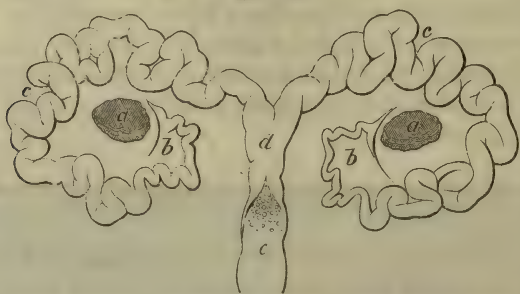
soon, the external layers of the albumen liquefy; and the vitellus, being specifically lighter than the albumen, rises toward the surface of the egg, with the cicatricula uppermost. This part presents itself almost immediately on breaking open the egg at any point corresponding to the equator of the yolk, and is placed in the most favorable position for the action of warmth and atmospheric air in the development of the chick.

The vitellus, therefore, is still the essential constituent part, even in the large and highly complicated fowl's egg; while the remainder con-

sists of nutritious material, provided for the support of the embryo, and of protective envelopes, like the shell and fibrous membranes.

In the quadrupeds, another important modification of the oviducts takes place. In these animals, the egg, which is originally of minute size, is retained within the generative passages of the female during the development of the embryo. While the upper part of the oviduct, accordingly, is quite narrow, and serves merely to transmit the egg from the ovary, and to supply it with a little albuminous secretion, the lower portions are much increased in size, and are lined with a mucous membrane which is adapted to provide for the protection and nourishment of the embryo during gestation. The upper and narrower portions of the oviduct are known as the "Fallopian tubes," from Fallopius[1] who first described them in the human female; while the lower and

Fig. 228.



Uterus and Ovaries of the Sow.—*a, a.* Ovaries. *b, b.* Fallopian tubes. *c, c.* Horns of the uterus. *d.* Body of the uterus. *e.* Vagina.

more highly developed portions constitute the uterus. The two halves of the uterus unite with each other upon the median line near their inferior termination, to form a central organ, termed its "body;" while the ununited parts are known as its "cornua" or "horns."

In the human species, the ovaries consist of Graafian follicles, imbedded in a somewhat dense connective tissue, supplied with an abundance of bloodvessels, and covered with an opaque, yellowish-white layer of fibrous tissue, called the "albugineous tunic." Over the whole is a layer of peritoneum, which is reflected upon the bloodvessels supplying the ovary, and is continuous with the broad ligaments of the uterus; but which elsewhere is closely consolidated with the albugineous tunic.

The oviducts commence by a wide expansion, provided with fringed edges, called the "fimbriated extremity of the Fallopian tube." The Fallopian tubes themselves are narrow and convoluted, terminating, on each side, in the upper part of the body of the uterus. The body of the uterus, in the human species, is so much developed at the expense of the cornua, that the latter hardly appear to have an existence, and no trace of them is visible externally. But on opening the uterus, its cavity is

[1] Opera Omnia. Francofurti, 1600. Observationes Anatomicæ, p. 421.

seen to be somewhat triangular in shape, its two superior angles running out to join the lower extremities of the Fallopian tubes. This portion evidently consists of the cornua, which have been consolidated with the body of the uterus, and enveloped in its thickened layer of muscular fibres.

Fig. 229.

GENERATIVE ORGANS OF THE HUMAN FEMALE.—*a*, *a*. Ovaries. *b*, *b*. Fallopian tubes. *c*. Body of the uterus. *d*. Cervix. *e*. Vagina.

The cavity of the body of the uterus terminates below by a constricted portion, termed the os internum, by which it is separated from the cervix. These two cavities are not only different from each other in shape, but also in the structure of their mucous membrane and in the functions which they perform.

The mucous membrane of the body of the uterus in its usual condition is smooth and rosy in color, and closely adherent to the subjacent muscular tissue. It consists of tubular follicles, ranged side by side, and opening by distinct orifices upon its free surface. The secretion of these follicles is destined for the nutrition of the embryo during the earlier periods of its formation.

The internal surface of the cervix, on the other hand, is raised in prominent ridges, arranged usually in two lateral sets, diverging from a central longitudinal ridge; presenting the appearance known as the "arbor vitæ uterina." The follicles of this part of the uterine mucous membrane are of a globular or sac-like form, and secrete a tenacious mucus, which serves, during gestation, to block up the cavity of the cervix, and thus to prevent the escape or injury of the egg.

The cavity of the cervix uteri is terminated inferiorly by a second constriction, the "os externum;" and below this comes the vagina, which constitutes the last division of the female generative passages.

The accessory female organs of generation consist, therefore, of ducts or tubes, by means of which the egg is conveyed from within outward. These ducts vary in the degree and complication of their development,

in different kinds of animals, according to the importance of the function which they perform. In the lower orders, they serve mainly to convey the egg to the exterior, and to supply it more or less abundantly with an albuminous secretion; while in the mammalia and in man, they are adapted to the more important office of retaining the egg during the period of gestation, and of providing during the same time for the nourishment of the embryo.

CHAPTER IV.

THE SEMINAL FLUID, AND THE MALE ORGANS OF GENERATION.

THE mature egg is not by itself capable of being developed into the embryo. If simply discharged from the ovary and carried through the oviducts to the exterior, it soon dies and is decomposed, like any other portion of the body separated from its connections. It is only when fecundated by the seminal fluid of the male, that it is stimulated to continued development, and becomes capable of more complete organization.

The product of the male generative organs is a colorless, somewhat viscid, albuminous fluid, containing minute filamentous bodies, the *spermatozoa*. This name has been given to the bodies in question on account of their exhibiting, when recently discharged, a very active and continuous movement suggesting the idea of an independent animal organization.

Anatomical Characters of the Spermatozoa.—The spermatozoa of man (Fig. 230, *a*) are about .045 millimetre in length, according to the measurements of Kölliker. Their anterior extremity presents a somewhat flattened triangular-shaped enlargement, termed the "head," which constitutes about one-tenth part the entire length of the spermatozoon. The remaining portion is a slender filamentous prolongation, called the "tail," which tapers gradually backward, becoming so exceedingly delicate toward its extremity, that it is difficult to be seen except when in motion. There is no further organization visible in any part of the spermatozoon; and the whole appears to consist, so far as can be seen by the microscope, of a homogeneous substance. The terms head and tail, as remarked by Bergmann and Leuckart,[1] are not used, when describing the different parts of the spermatozoon, in the same sense as that in which they would be applied to the corresponding parts of an animal; but simply for the sake of convenience, as one might speak of the head of an arrow or the tail of a comet.

In the lower vertebrate animals, the spermatozoa have the same general form as in man; that is, they are filamentous bodies, with the anterior extremity more or less enlarged. In the rabbit, the head is roundish and flattened in shape, somewhat resembling a blood globule. In the rat (Fig. 230, *b*) they are much larger than in man, measuring nearly 0.20 millimetre in length. The head is of a conical form, about one-

[1] Vergleichende Physiologie. Stuggart, 1852.

Fig. 230.

SPERMATOZOA.—*a.* Human. *b.* Of the rat. *c.* Of Menobranchus. Magnified 480 times.

twentieth the whole length of the filament, and often slightly curved at its anterior extremity. In the frog and in reptiles generally, the spermatozoa are longer than in quadrupeds. In Menobranchus, the great American water-lizard, they are of very unusual size (Fig. 230, *c*), measuring not less than 0.57 millimetre in length, about one-third of which is occupied by the head, or enlarged portion of the filament.

The most remarkable peculiarity of the spermatozoa, as seen under the microscope, is their rapid and energetic movement. In a drop of fresh seminal fluid, if kept sufficiently moistened and at its normal temperature, the numberless filaments with which it is crowded are seen to be in a state of incessant motion. In many species of animals, the movement of the spermatozoa strongly resembles that of a tadpole; particularly when, as in the mammalia, they consist of a short, well-defined head, followed by a long and slender tail. The tail-like filament keeps up a constant lateral vibratory movement, by which the spermatozoon is driven from place to place in the seminal fluid, as a fish or a tadpole is propelled through the water. In other instances, as in the Triton, or water lizard, the spermatozoa have a continuous writhing or spiral-like movement; presenting a peculiarly elegant appearance when large numbers are viewed together.

It is this movement which gave origin to the name of spermatozoa, to designate the filaments of the spermatic fluid. But, notwithstanding its active character, and its resemblance in mechanism to the locomotion of certain animals, it has no analogy with a voluntary act.

The spermatozoa are organic forms, produced in the testicles, and constituting a part of their tissue; just as the eggs, which are produced in the ovaries, naturally form a part of the texture of these organs. Like the egg, the spermatozoon is destined to be discharged from the organ where it grew, and to retain, for a certain time afterward, its vital properties. One of these properties is its power of movement; but this does not indicate the possession of independent vitality, and is not even necessarily a proof of its animal origin. The move-

ment of a spermatozoon is not more active than that of a bacterium cell, or that of the ciliated zoospores of certain fresh-water algæ. It is more strictly analogous to the motion of a ciliated epithelium cell when detached from its mucous membrane, which will sometimes continue for many hours, if kept under favorable conditions of temperature and moisture. The power of movement manifested by the spermatozoa also continues for a time after their separation from the rest of the body; but it is limited in duration, and after a certain interval comes to an end.

In order to preserve their vitality, the spermatozoa must be kept at or near the normal temperature of the body, and preserved from the contact of air or other unnatural fluids. If the seminal fluid be allowed to dry, or if it be diluted by water, in the case of birds and quadrupeds, or if it be subjected to extremes of heat or cold, the motion ceases, and the spermatozoa soon begin to disintegrate.

Formation of the Spermatozoa.—The spermatozoa are produced in the interior of certain glandular-looking organs, the *testicles*, which are characteristic of the male, as the ovaries are characteristic of the female. In man and mammalia, the testicles are solid, ovoid-shaped bodies, composed of long, narrow, convoluted tubes, the "seminiferous tubes," somewhat similar to the tubuli uriniferi of the kidneys. They lie for the most part closely in contact with each other, nothing intervening between them except capillary bloodvessels and a little connective tissue. They commence, by rounded extremities, near the external surface of the testicle and pursue an intricately convoluted course toward its central and posterior part. They are not strongly adherent to each other, but may be readily unravelled by manipulation.

According to the investigations of Kölliker, the formation of the spermatozoa takes place within peculiar cells occupying the cavity of the seminiferous tubes. As the age of puberty approaches, beside the ordinary pavement epithelium lining the tubes, other cells or vesicles of larger size make their appearance, each containing from one to fifteen or twenty nuclei, with nucleoli. In the interior of these vesicles spermatozoa are formed; their number corresponding usually with that of the nuclei. They are developed in bundles of from ten to twenty, held together by the membranous substance surrounding them, but are afterward set free by the liquefaction of the vesicle, and then nearly fill the cavity of the seminiferous ducts, being mingled only with a minute quantity of transparent fluid.

While in the seminiferous tubes, the spermatozoa are always inclosed in their parent vesicles; they are liberated, and mingled together, only after entering the rete testis and the head of the epididymis.

Accessory Male Organs of Generation.—Beside the testicles, which are the essential parts of the male generative apparatus, there are certain accessory organs, by which the seminal fluid is conveyed to the exterior, and mingled with various secretions which assist in the accomplishment of its function.

As the sperm leaves the testicle, it consists almost entirely of spermatozoa, crowded together in an opaque, white, semi-fluid mass, which fills the vasa efferentia, and distends their cavities. It then enters the single duct which forms the body and lower extremity of the epididymis, following the long and tortuous course of this tube, until it reaches the vas deferens; through which it is conveyed onward to the vesiculæ seminalis. Throughout this course, it is mingled with a scanty mucus-like fluid, secreted by the walls of the epididymis and vas deferens. The vesiculæ seminales contain also a glairy fluid, produced by secretion from their walls, which serves some secondary purpose in completing the formation of the sperm. One of its functions is no doubt to dilute the mass of spermatozoa, as they arrive from the testicles, and thus allow them liberty of motion; as well as to increase the volume of the seminal fluid and enable it to be expelled by the muscular contraction of the parts about the urethra. Kölliker has found that the spermatozoa in the vas deferens and epididymis are generally motionless; and that they exhibit their characteristic movements only in the vesiculæ seminales and in the ejaculated sperm.

At the moment of the final evacuation of the sperm, it first passes from the vesiculæ seminales into the prostatic portion of the urethra, where it meets with the secretion of the prostate gland, which is then poured out in unusual abundance; and farther on, there are added the secretions of Cowper's glands and of the remaining mucous follicles of the urethra. All these fluids increase the quantity of the sperm, and serve as vehicles for the transport of the spermatozoa.

Necessary Conditions of Fecundation by the Seminal Fluid.—There are several conditions which are essential to the successful accomplishment of the act of fecundation.

First, the spermatozoa must be present and in a state of active vitality. Of all the organic ingredients, derived from different sources, which go to make up the mixed seminal fluid, as discharged from the urethra, it is the spermatozoa which constitute its essential part. They are the true fecundating element of the sperm, while the others are of secondary importance, and perform only accessory functions.

Spallanzani[1] found that if frog's sperm be passed through a succession of filters, so as to separate the solid from the liquid portions, the filtered fluid is destitute of fecundating properties; while the spermatozoa entangled in the filter, if mixed with a sufficient quantity of fluid of the requisite density for dilution, may still be successfully used for the artificial impregnation of eggs. It is well known that animals or men, after removal of both testicles, are incapable of impregnating the female, notwithstanding that all the other generative organs may remain uninjured. The seminal fluid, furthermore, must be in a fresh condition, so that the spermatozoa retain their anatomical characters and their active movement. The experiments of Spallanzani have shown that,

[1] Expériences pour servir à l'Histoire de la Génération. Genève, 1786.

if the above conditions be preserved, the seminal fluid, removed from the spermatic ducts of the male, is capable of fecundating the eggs of the female. But if allowed to remain exposed to the atmosphere, or to an unnatural temperature, it becomes inert. So long as the spermatozoa continue in active motion, they are usually found to retain their physiological properties; the cessation of this movement, on the other hand, being a sign that their vitality is exhausted, and that they are no longer capable of impregnating the egg.

Secondly, both eggs and spermatozoa must have arrived at a certain degree of development before fecundation can take place. Previous to this time the immature eggs are incapable of being impregnated, and the imperfectly developed spermatozoa have not yet acquired their fecundating power. The necessary process of growth takes place within the generative organs; and when it is complete, both the spermatozoa of the male and the eggs of the female are ready to be discharged, and are in condition to exert upon each other the necessary influence.

The fecundating power of the spermatozoa, when fully developed, is exceedingly active. Spallanzani found that one-fifth of a gramme of the seminal fluid of the frog, diffused in water, was sufficient for the impregnation of several thousand eggs. The process seems to be accomplished almost instantaneously, "since eggs which were allowed to remain in the fecundating mixture for only one second proved to be impregnated, and were afterward hatched at the usual period."

Thirdly, the spermatozoa must come into direct contact with the egg or its immediate envelopes. Spallanzani first demonstrated this by attaching mature eggs to the concave surface of a watch-glass, which he placed, in an inverted position, over a second watch-glass containing fresh seminal fluid. The eggs, allowed to remain in this way for several hours, exposed to the vapor of the fluid but without touching its surface, were afterward found to have failed of impregnation; while others, which were actually moistened with the same seminal fluid, became developed into living tadpoles.

Finally, the physiological act of fecundation is accomplished by the entrance of the spermatozoa into the interior of the egg, through the vitelline membrane, and their union with the substance of the vitellus. This fact was first observed by Martin Barry[1] in the fecundated egg from the Fallopian tube of the rabbit. It has subsequently been seen by Newport[2] in the frog, by Bischoff, by Coste, by Robin[3] in a species of leech, by Flint[4] in the pond snail, and by Weil,[5] in repeated instances, in the rabbit. According to some of these observations, the mechanism of penetration is by means of a natural orifice or "micropyle" existing in

[1] Philosophical Transactions. London, 1840, p. 533, and 1843, p. 33.

[2] Philosophical Transactions, 1853, p. 271.

[3] Journal de la Physiologie de l'Homme et des Animaux. Paris, 1862, tome v. p. 80.

[4] Physiology of Man. New York, 1874, vol. v. p. 352.

[5] Stricker's Medizinischer Jahrbücher. Wien, 1873, p. 18.

the vitelline membrane, as first indicated by Barry. In others no such orifice has been visible; the spermatozoa appearing to perforate the substance of the vitelline membrane by the impulsive movement of their filamentous extremity (Newport). Such a mode of penetration is not inadmissible, since the much larger embryos of the tænia and trichina (page 675) make their way without difficulty through the substance of the intestinal mucous membrane.

After their arrival in the interior of the vitelline cavity, the spermatozoa disappear as distinct organic elements. Their substance unites with that of the vitellus; and thenceforward the fecundated egg consists of materials derived from both the male and female organisms. The greater portion of this material is that produced by the female; but that which is supplied from the seminal filaments of the male is equally essential for the production of an embryo. The offspring, accordingly, may exhibit resemblances to either or both of the individual parents, since it originates from a union of both the generative products.

Union of the Sexes.—In most of the lower animals there is a periodical development of the testicles in the male, corresponding in time with that of the ovaries in the female. As the ovaries enlarge and the eggs ripen in the one sex, so in the other the testicles increase in size, as the season of reproduction approaches, and become turgid with spermatozoa. The accessory organs of generation at the same time share the unusual activity of the testicles, and become increased in vascularity and ready to perform their part in the reproductive function.

In fishes, as a general rule, where the testicles occupy, in the abdomen of the male, the same relative position as the ovaries in the female, these organs enlarge, become distended with their contents, and project into the peritoneal cavity. Each of the two sexes is then at the same time under the influence of a corresponding excitement. The unusual development of the reproductive organs reacts upon the general system, and produces a state of peculiar excitability, known as the condition of "erethism." The female, distended with eggs, feels the stimulus which leads to their expulsion; while the male, bearing the weight of the enlarged testicles and the accumulation of newly-developed spermatozoa, is impelled by a similar sensation to the discharge of the seminal fluid. The two sexes are led by instinct at this season to frequent the same situations. The female deposits her eggs in some spot favorable to the protection and development of the young; after which the male, apparently attracted and stimulated by the sight of the new-laid eggs, discharges upon them the seminal fluid, and their impregnation is accomplished. It is in this way that fecundation takes place in nearly all the osseous fishes, as the trout, the salmon, and the stickleback.

In instances like the above, where the male and female generative products are discharged separately, the subsequent contact of the seminal fluid with the eggs would seem to be dependent on the occurrence of fortuitous circumstances, and their impregnation, therefore, liable to

fail. But, in point of fact, the simultaneous functional excitement of the two sexes, and the operation of corresponding instincts, leading them to ascend the same rivers and to frequent the same spots, provide with sufficient certainty for the impregnation of the eggs. The number of eggs produced by the female is also very large, the ovaries being often so distended as nearly to fill the abdominal cavity; so that, although many of the eggs may be accidentally lost, a sufficient number will still be impregnated to provide for the continuation of the species.

In many of the cartilaginous fishes, on the other hand, as in sharks, rays, and skates, an actual contact takes place between the two sexes at the time of reproduction, and the seminal fluid of the male is introduced into the generative passages of the female. Thus the eggs are fecundated while still in the body of the female, and in many species go through with a nearly complete development in this situation and are born alive.

In the frog, the male fastens himself upon the back of the female by means of the anterior limbs, which retain their hold by a kind of spasmodic contraction. This continues for one or more days, during which time the mature eggs, which have been discharged from the ovary, are passing downward through the oviducts. As they are expelled from the anus, the seminal fluid of the male is discharged upon them, and impregnation takes place.

In serpents, lizards, and turtles, the sperm is introduced into the female generative passage at the time of copulation, by means of a single or double erectile male organ. Of these animals, some species lay their eggs immediately after fecundation, others retain them until the embryo is partly or fully developed.

In birds, the spermatozoa are introduced into the sexual orifice of the female, and make their way into the upper portion of the oviduct, where they may be found in active motion, mingled with the fluids of this canal.[1] The vitellus is thus fecundated immediately upon its discharge from the ovary, and before it has become surrounded with the albuminous and membranous envelopes supplied by the middle and lower portions of the oviduct.

Lastly, in the human species and in mammalians, where the impregnated egg is to be retained in the body of the female parent during the whole period of its development, the seminal fluid is introduced into the vagina and uterus by sexual congress, and meets the egg at or soon after its discharge from the ovary. A close correspondence between the periods of sexual excitement, in the male and the female, is visible in many of these animals, as well as in fish, birds, and reptiles. This is the case in most species which produce young but once a year, as the deer, the wolf, and the fox. In others, such as the dog, the rabbit, and the guinea pig, where several broods of young are produced during the year, or where, as in man, the generative epochs of the female recur at short intervals, the time of impregnation is comparatively indefinite,

[1] Foster and Balfour, Elements of Embryology. London, 1874, p. 21.

and the generative apparatus of the male is almost constantly in a state of full development. It is excited to action at particular periods, apparently by some influence derived from the condition of the female.

In quadrupeds and in the human species, the contact of the sperm with the egg, and the fecundation of the latter, take place in the generative passages of the female; either in the uterus, the Fallopian tubes, or upon the surface of the ovary; in each of which situations the spermatozoa have been found, after the accomplishment of sexual intercourse.

CHAPTER V.

PERIODICAL OVULATION, AND THE FUNCTION OF MENSTRUATION.

I. Periodical Ovulation.

The periodical ripening of the eggs and their discharge from the generative organs constitute the process, known by the name of "ovulation," which may be considered as the primary act of reproduction. The characteristic phenomena which distinguish the performance of this function depend upon the following general laws, which apply with but little variation to all classes of animals.

1st. *Eggs exist originally in the ovaries, as part of their natural structure.* In fish, reptiles, and birds, the ovary is of comparatively simple texture, consisting only of a number of Graafian follicles, united by an intervening stroma of loose connective tissue, and thus aggregated into the form of a rounded, elongated, or lobulated organ. In the mammalians and in man, its essential constitution is the same; but its connective tissue is denser and more abundant, and the figure of the organ is more compact. But in all classes the interior of each Graafian follicle is occupied by an egg, from which the embryo is afterward produced.

The process of reproduction was formerly regarded as essentially different in the oviparous and the viviparous animals. In oviparous animals, such as most fishes and reptiles and all birds, the young animal was well known to be formed from an egg produced by the female; while in the viviparous species, or those which bring forth their young alive, as certain fishes and reptiles and all the mammalians, the embryo was supposed to originate in the body of the female in consequence of sexual intercourse. But by the aid of the microscope, as employed in the examination of the different organs and tissues, it was subsequently found that, in mammalians also, the ovaries contain eggs. The mammalian eggs had previously escaped observation owing to their comparatively simple structure and minute size; but they were nevertheless found to possess all the essential characters belonging to the larger eggs of the oviparous animals.

The true difference in the process of reproduction, between the two classes, is therefore merely an apparent, not a fundamental one. In the oviparous fish, reptiles, and birds, the egg is discharged by the female before or immediately after impregnation, and the embryo is subsequently developed and hatched externally. In quadrupeds and in the human species, on the other hand, the egg is retained within the body

of the female until the embryo is developed; and the membranes are ruptured and the young expelled at the same time. In all classes, viviparous as well as oviparous, the young is produced from an egg; and in all classes the egg, sometimes larger and sometimes smaller, but always consisting essentially of a vitellus and a vitelline membrane, is contained originally in the interior of an ovarian follicle.

The egg is accordingly an integral part of the ovarian tissue. It exists there long before the generative function is established, and during the earliest periods of life. It may be found without difficulty in the newly born female infant, and may even be detected in the fœtus before birth. Its growth and nutrition are provided for in the same manner with that of other portions of the bodily structure.

2d. *The ovarian eggs become more fully developed at a certain age when the generative function is about to be established.* During the early periods of life, the ovaries and their contents, like many other organs, are imperfectly developed. They exist, but they are as yet inactive and incapable of performing their special function. In the young chick, for example, the ovary is of small size; and the eggs, instead of presenting the voluminous, yellow, opaque vitellus which they afterward exhibit, are minute, transparent, and colorless. In young quadrupeds, and in the human female during infancy and childhood, the ovaries are equally inactive. They are small, friable, and of a nearly homogeneous appearance to the naked eye; presenting none of the enlarged follicles, filled with transparent fluid, which afterward become a characteristic feature of the organ. At this time, accordingly, the female is incapable of bearing young, because the ovaries are inactive, and the eggs which they contain immature.

But at a certain period, which varies in the time of its occurrence for different species of animals, the sexual apparatus begins to enter upon a state of activity. The ovaries increase in size, and their circulation becomes more active. The eggs, which have previously remained quiescent, take on a rapid growth, and the structure of the vitellus is completed by a deposit of semi-opaque granular matter in its interior. Arrived at this state, the eggs are ready for impregnation, and the female becomes capable of bearing young. She is then said to have arrived at the state of "puberty," or that condition in which the generative organs are fully developed. This change is accompanied by a visible alteration in the system at large, which indicates the complete development of the entire organism. In many birds, the plumage assumes at this period more varied and brilliant colors; and in the common fowl, the comb, or "crest," enlarges and becomes red and vascular. In the American deer (Cervus virginanus), the coat, which during the first year is mottled with white, becomes in the second year of a uniform tawny or reddish tinge. In nearly all species, the limbs become more compact and the body more rounded; and the whole external appearance is so altered, as to indicate that the animal has arrived at the period of puberty, and is capable of reproduction.

3d. *Successive crops of eggs, in the adult female, ripen and are discharged independently of sexual intercourse.* The original formation of the germ, in the bodies of viviparous animals, was formerly supposed to be a consequence of sexual intercourse. Even after it became known that the ovaries of these animals contain eggs before impregnation, the discharge of the egg from its follicle was thought to occur only under the influence of fecundation; and the rupture of a follicle was consequently regarded as an indication that sexual intercourse had taken place.

But subsequent observation showed that not only the existence, but also the ripening and discharge of the egg, are phenomena dependent on the structure and functional activity of the female organism. In many fish and reptiles, the mature eggs leave the ovary, pass through the oviducts, and are discharged externally before coming in contact with the seminal fluid of the male. In the domestic fowl it is a matter of common observation that the hen, if well supplied with nourishment, will continue to lay fully formed eggs without the presence of the cock; only these eggs, not having been fecundated, are incapable of producing chicks. In oviparous animals, therefore, the discharge of the egg, as well as its formation, may take place independently of sexual intercourse.

This is also the case in the viviparous quadrupeds. The observations of Bischoff, Pouchet, and Coste, on the sheep, the pig, the bitch, and the rabbit, have demonstated that if the female be carefully kept from the male until after the period of puberty is established, and then killed, examination of the ovaries will sometimes show that Graafian follicles have matured, ruptured, and discharged their eggs, though no sexual intercourse has taken place. Sometimes the follicles are found distended and prominent upon the surface of the ovary; sometimes recently ruptured and collapsed; and sometimes in various stages of cicatrization and atrophy. Bischoff,[1] in several instances of this kind, found the unimpregnated eggs in the oviduct, on their way to the cavity of the uterus. In species of animals where the ripening of the eggs takes place at short intervals, as in the sheep, the pig, or the cow, it is very rare to examine the ovaries where traces of a more or less recent rupture of the Graafian follicles are not distinctly visible.

One of the most important facts, derived from these observations, is that the ovarian eggs become developed and are discharged in successive crops, which follow each other at periodical intervals. In the ovary of the fowl (Fig. 226), it may be seen at a glance that the eggs grow and ripen, one after the other, like fruit upon a vine. In this instance, the process of evolution is rapid; and it is easy to distinguish, at the same time, eggs which are almost microscopic in size, colorless, and transparent; those which are larger, somewhat opaline, and yellowish

[1] Mémoire sur la chûte périodique de l'œuf, Annales des Sciences Naturelles, Paris, Août—Septembre, 1844.

in hue; and finally those which are fully developed, opaque, of a deep orange color, and nearly ready to leave the ovary.

Here, the difference between the undeveloped and the mature eggs consists mainly in the size of the vitellus, which is very much larger than in the quadrupeds. The ovarian follicle is distended and ruptured, and the egg finally discharged, owing to the pressure exerted by the increased size of the vitellus.

In man and mammalians, on the other hand, the microscopic egg never becomes large enough to distend the Graafian follicle by its own size. The rupture of the follicle and the liberation of the egg are accordingly provided for, in these instances, by a different mechanism.

In the earlier periods of life, in man and the mammalians, the egg is contained in a Graafian follicle which closely embraces its exterior, and is consequently hardly larger than the egg itself. As puberty approaches, the follicles situated near the free surface of the ovary become enlarged by the accumulation of serous fluid in their cavity. At that time, the ovary, if cut open, shows a considerable number of globular, transparent vesicles, the smaller of which are deep seated, but which increase in size as they approach the free surface of the organ. These are the Graafian follicles, which, in consequence of the advancing maturity of their eggs, gradually enlarge at the arrival of the period of generation.

The Graafian follicle then consists of a closed globular sac, the external wall of which, though quite translucent, has a fibrous texture, and is well supplied with bloodvessels. This fibrous and vascular wall is distinguished by the name of the "vesicular membrane." It is not very firm in texture, and if roughly handled is easily ruptured.

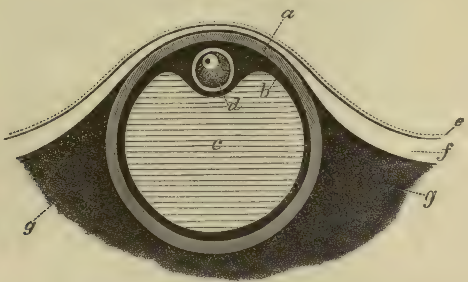
The vesicular membrane is lined throughout by a layer of minute granular cells, which form for it a kind of epithelium. This layer is termed the *membrana granulosa.* It adheres but slightly to the vesicular membrane, and may easily be detached by careless manipulation before the follicle is opened, being then mingled, in the form of light flakes and shreds, with the serous fluid contained in its interior.

At the most superficial part of the Graafian follicle the membrana granulosa is thicker than elsewhere. Its cells are here accumulated, in a kind of mound or "heap," which has received the name of the *cumulus proligerus.* It is also called the *discus proligerus*, because the thickened mass, when viewed from above, has a nearly circular or disk-like form. In the centre of this thickened portion of the membrana granulosa the egg is imbedded. It is accordingly always situated at the most superficial portion of the follicle, and advances in this way toward the surface of the ovary.

As the period approaches at which the egg is to be discharged, the Graafian follicle becomes more vascular, and enlarges by an increased exudation into its cavity. It then begins to project from the surface of the ovary, still covered by the albugineous tunic and its peritoneal

investment. (Fig. 231.) The constant accumulation of fluid in the follicle exerts such a pressure from within outward, that the albugineous

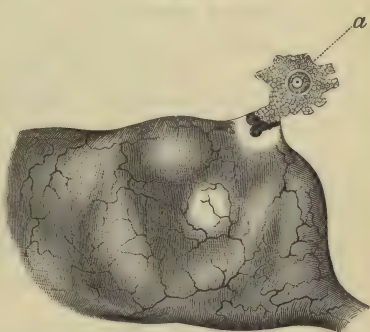
Fig. 231.



GRAAFIAN FOLLICLE, near the period of rupture.—*a.* Vesicular membrane. *b.* Membrana granulosa. *c.* Cavity of follicle. *d.* Egg. *e.* Peritoneal surface. *f.* Tunica albuginea. *g, g.* Tissue of the ovary.

tunic and the peritoneum gradually yield before it; until the Graafian follicle protrudes from the ovary as a tense, rounded, translucent vesicle, in which fluctuation can be readily perceived on applying the fingers to its surface. Finally, the process of effusion and distension still going on, the wall of the vesicle yields at its most prominent portion, the contained fluid is driven out with a gush, by the elastic reaction of the ovarian tissue, carrying with it the egg, still entangled in the cells of the membrana granulosa.

Fig. 232.



OVARY WITH GRAAFIAN FOLLICLE RUPTURED: at *a*, the egg, just discharged, with a portion of the membrana granulosa.

The rupture of the Graafian follicle is accompanied, in some instances, by hemorrhage from its internal surface, by which its cavity is filled with blood. This occurs in the human species, also in the pig, and to some extent in several other of the lower animals. Sometimes, as in the cow, where no immediate hemorrhage takes place, the Graafian follicle, when ruptured, simply collapses; after which a slight exudation, more or less tinged with blood, is poured out during the course of a few hours.

This process occurs in one or more Graafian follicles at a time, according to the number of young produced at a birth. In the bitch and the sow, where each litter consists of from six to twenty young ones, a similar number of eggs ripen and are discharged at each period. In the mare, in the cow, and in the human female, where there is usually but one

fœtus at a birth, the eggs are matured singly, and the Graafian follicles ruptured, one after the other, at successive periods of ovulation.

4th. *The ripening and discharge of the egg are accompanied by a peculiar condition of the general system, known as the "rutting" condition, or "œstruation."* The congestion and functional activity manifested by the ovaries at each period of ovulation, act by sympathy upon the other generative organs and produce in them a greater or less degree of excitement, according to the particular species of animal. Usually there is a certain amount of congestion of the entire generative apparatus. The secretions of the vagina and neighboring parts are more particularly affected, being increased in quantity and altered in quality. In the bitch, the vaginal mucous membrane becomes red and tumefied, and pours out a secretion which is more or less tinged with blood. The vaginal secretions acquire at this time a peculiar odor, which appears to attract the male, and to excite in him the sexual impulse. An unusual tumefaction and redness of the vagina and vulva are also perceptible in the rabbit; and in some species of apes there is not only a bloody discharge from the vulva, but also an engorgement and infiltration of the neighboring parts, extending to the skin of the buttocks, the thighs, and the under part of the tail.[1]

The system at large is also visibly affected by the process going on in the organs of generation. In the cow, the approach of an œstrual period is marked by unusual restlessness. The animal partially loses her appetite. She frequently stops browsing, looks about uneasily, runs from one side of the field to the other, and then recommences feeding, to be disturbed again in a similar manner after a short interval. The motions are rapid and nervous, and the hide often rough and disordered; and the whole aspect of the animal indicates the presence of some special excitement. After œstruation is fully established, the vaginal secretions show themselves in unusual abundance, and so continue for one or two days; after which the symptoms subside, and the animal returns to her usual condition.

It is a noticeable fact, in this connection, that the female of these animals will allow the approach of the male only during and immediately after the œstrual period; that is, when the egg is recently discharged, and ready for impregnation. At other times, when sexual intercourse would be necessarily fruitless, the instinct of the animal leads her to avoid it; and the concourse of the sexes is accordingly made to correspond in time with the maturity of the egg and its aptitude for fecundation.

II. Menstruation.

In the human female, the return of the period of ovulation is marked by a group of phenomena which are known as *menstruation*, and which are of sufficient importance to be described by themselves.

[1] Pouchet, Théorie positive de l'ovulation. Paris, 1847, p. 230.

During infancy and childhood the sexual system is inactive. No discharge of eggs takes place from the ovaries, and no external phenomena show themselves, connected with the reproductive function.

But at the age of fourteen or fifteen years, a change begins to manifest itself. The limbs become rounder, the breasts increase in size, and the entire aspect undergoes a peculiar alteration, which indicates approaching maturity. At the same time a discharge of blood takes place from the generative passages, accompanied by some disturbance of the general system, and the female is then known to have arrived at the period of puberty.

Afterward, the bloody discharge returns at regular intervals of four weeks; and, on account of this recurrence, corresponding with successive lunar months, its phenomena are designated by the name of the "menses" or the "menstrual periods." The menses return with regularity, from the time of their first appearance, until the age of about forty-five years. During this period, the female is capable of bearing children, and sexual intercourse is liable to be followed by pregnancy. After the forty-fifth year, the periods first become irregular, and then cease altogether; and their final disappearance is an indication that pregnancy cannot again take place.

During the period above referred to, from the age of fifteen to forty-five years, the regularity and completeness of the menstrual periods indicate to a great extent the aptitude of individual females for impregnation. All causes of ill health which derange menstruation are apt at the same time to interfere with pregnancy; so that women whose menses are regular and natural are more likely to become pregnant, after sexual intercourse, than those in whom the periods are absent or irregular.

If pregnancy happen to take place, however, at any time within the normal period, the menses are suspended during its continuance. They usually remain absent, after delivery, until the end of lactation, when they recommence, and continue to recur at their regular periods, as before.

The menstrual discharge consists of mucus mingled with blood. When the period is about to come on, the female is affected with a certain degree of discomfort and lassitude, a sense of weight in the pelvis, and more or less disinclination to society. These symptoms are in some instances slightly pronounced, in others more troublesome. An unusual discharge of vaginal mucus then begins to take place, soon becoming yellowish or rusty brown in color, from the admixture of a certain proportion of blood; and by the second or third day the discharge has the appearance of nearly pure blood. The unpleasant sensations, at first manifest, then usually subside; and the discharge, after continuing for two or three days longer, grows more scanty. Its color changes from red to a brownish or rusty tinge, until it finally disappears altogether, and the period comes to an end.

The menstrual epochs of the human female correspond with the

periods of œstruation in the lower animals. Their general resemblance to these periods is very evident. Like them, they are absent in the immature female, and begin to take place only at the period of puberty, when the aptitude for impregnation commences. Like them, they recur during the child-bearing period at regular intervals, and are liable to the same interruption by pregnancy. Finally, their disappearance corresponds with the cessation of fertility.

The periods of œstruation, in many of the lower animals, are accompanied with an unusual discharge from the generative passages, frequently more or less tinged with blood. In the human female the bloody discharge, though more abundant than in other instances, differs only in degree from that in many species of animals.

But the most complete evidence that the period of menstruation is in reality that of ovulation, is derived from the results of direct observation. A sufficient number of instances have been observed to show that at the menstrual epoch a Graafian follicle becomes enlarged, ruptures, and discharges its egg. Cruikshank[1] noticed such a case so long ago as 1797. Négrier[2] relates two instances in which, after sudden death during menstruation, a bloody and ruptured Graafian follicle was found in the ovary. Bischoff[3] speaks of four similar cases, in three of which the follicle was just ruptured, and in the fourth distended, prominent, and ready to burst. Coste[4] met with several of the same kind. Michel[5] found a follicle ruptured and filled with blood in a woman who was executed for murder while the menses were present. Two instances are reported by Letheby,[6] in women who died while under observation in the London hospitals, in one of which he succeeded in finding the ovum, which had been expelled from the ovary, in the contents of the corresponding Fallopian tube. We have also seen a Graafian follicle recently ruptured and filled with blood, in a woman who died on the second day of menstruation.

Ovulation, accordingly, in the human female, accompanies and forms a part of menstruation. As the menstrual period comes on, a congestion takes place in nearly the whole of the generative apparatus; in the Fallopian tubes and the uterus, as well as in the ovaries and their contents. One of the Graafian follicles is especially the seat of vascular excitement. It becomes distended by the fluid accumulated in its cavity, projects from the surface of the ovary, and is finally ruptured; the process taking place essentially in the same manner as in the mammalian animals.

It is not certain at what particular period of the menstrual flow the rupture of the follicle and discharge of the egg take place. According

[1] Philosophical Transactions. London, 1797, p. 135.

[2] Recherches sur les Ovaires. Paris, 1840, p. 78.

[3] Annales des Sciences Naturelles. Paris, Août, 1844.

[4] Histoire du Développement des Corps Organisés. Paris, 1847, tome i. p. 221.

[5] American Journal of the Medical Sciences. Philadelphia, July, 1848.

[6] Philosophical Transactions. London, 1852, p. 57.

to the observations of Bischoff, Pouchet, and Raciborski, the regular time for this rupture and discharge is not at the commencement, but toward the termination of the period. According to those of Coste,[1] the follicle ruptures sometimes in the early part of the menstrual epoch, sometimes later. So far as we can learn, therefore, the precise period is not invariable. Like the menses themselves, it may take place a little earlier, or a little later, according to circumstances; but it always occurs in connection with the menstrual flow, and constitutes the essential part of the catamenial process.

The egg, when discharged from the ovary, enters the fimbriated extremity of the Fallopian tube, and commences its passage toward the uterus. The mechanism by which it finds its way into and through the Fallopian tube is different, in quadrupeds and the human species, and in birds and reptiles. In the latter, the bulk of the egg or eggs is so great as to fill or even to distend the cavity of the oviduct; and the mass is accordingly embraced by the muscular wall of the canal and carried downward by its peristaltic action. In the mammalians, on the other hand, the egg is microscopic in size. The wide extremity of the Fallopian tube, directed toward the ovary, is lined with ciliated epithelium; and the movement of the cilia, which is from the ovary toward the uterus, produces a kind of vortex, by which the egg is drawn toward the narrow portion of the tube, and thence conducted to the cavity of the uterus.

Accidental causes may sometimes disturb the regular course of passage of the egg. It may be arrested at the surface of the ovary, and thus fail to enter the tube at all. If it be fecundated and go on to partial development in this situation, it will give rise to "ovarian pregnancy." The egg may escape from the fimbriated extremity of the Fallopian tube into the peritoneal cavity, and form attachments to a neighboring organ, causing "abdominal pregnancy;" or finally, it may stop in some part of the Fallopian tube, and so give origin to "tubal pregnancy."

The egg, immediately upon its discharge from the ovary, is ready for impregnation. If sexual intercourse take place about that time, the egg and the spermatozoa meet in some part of the female generative passages, and fecundation is accomplished. It appears from the observations of Bischoff, Coste, and Martin Barry[2] upon rabbits, that the contact between the egg and the spermatozoa may take place either in the uterus or any part of the Fallopian tubes, or even upon the surface of the ovary. If, on the other hand, sexual coitus do not take place, the egg passes down to the uterus unimpregnated, loses its vitality after a short time, and is carried away with the uterine secretions.

It is easily understood, therefore, why sexual intercourse should be more liable to be followed by pregnancy when occurring about the

[1] Histoire du Développement des Corps Organisés. Paris, 1847, tome i. p. 221.

[2] Philosophical Transactions. London, 1839, p. 315.

menstrual epoch than at other times. This fact, established as a matter of observation by practical obstetricians, depends upon the coincidence in time between the occurrence of menstruation and the discharge of the egg. Before its discharge, the egg is immature, and unfit for impregnation; and after the menstrual period has passed, it loses its freshness and vitality. The exact length of time, preceding and following the menses, during which impregnation is possible, has not been ascertained. The spermatozoa, on the one hand, retain their vitality for an unknown period after coition, and the egg for an unknown period after its discharge. Both these occurrences may either precede or follow each other within certain limits, and impregnation may still take place; but the precise extent of these limits is uncertain, and is probably more or less variable in different individuals.

The above facts indicate the true explanation of certain exceptional cases, in which fertility exists without menstruation. Various authors (Churchill, Reid, Velpeau) have related instances of fruitful women in whom the menses were scanty and irregular, or even entirely absent. The menstrual flow is only the external accompaniment of a more important process taking place within. It is habitually scanty in some individuals, and abundant in others. Such variations depend upon the condition of vascular activity of the system at large, or of the uterine organs in particular; and though the bloody discharge is usually an index of the general aptitude of these organs for impregnation, it is not an absolute or indispensable requisite. Provided a mature egg be discharged from the ovary at the appointed period, menstruation properly speaking exists, and pregnancy is possible.

The blood which escapes during the menstrual flow is supplied by the uterine mucous membrane. If the cavity of the uterus be examined after death during menstruation, its internal surface is found smeared with a sanguineous fluid, which may be traced through the uterine cervix into the vagina. The Fallopian tubes are sometimes congested, and filled with a similar bloody discharge. The menstrual blood has also been seen to exude from the uterine orifice in cases of procidentia uteri, as well as in the natural condition by examination with the vaginal speculum. It is discharged by a kind of capillary hemorrhage, and, as a general rule, does not form a visible coagulum, owing to its being gradually exuded from many minute points, and mingled with a large quantity of mucus. When poured out more rapidly or in larger quantity than usual, as in menorrhagia, the menstrual blood coagulates in the same manner as that derived from other sources. Its discharge takes place from the whole extent of the mucous membrane of the body of the uterus, and is, at the same time, the consequence and the natural termination of the periodical congestion of the parts.

CHAPTER VI.

THE CORPUS LUTEUM, AND ITS CONNECTION WITH MENSTRUATION AND PREGNANCY.

After the rupture of the Graafian follicle at the menstrual period, a bloody cavity is left in the ovary, which is subsequently obliterated by a kind of granulating process, somewhat similar to the healing of an abscess. The office of the Graafian follicle is to provide for the formation and growth of the egg within the ovary. After the ripening and discharge of the egg, the Graafian follicle has no longer any function to perform. It then only remains for it to pass through a process of obliteration, as an organ which has become obsolete. While undergoing this process, the Graafian follicle is at one time converted into a peculiar, solid, spheroidal body, called the *corpus luteum;* a name derived from the yellow color which it acquires at a certain period of its formation.

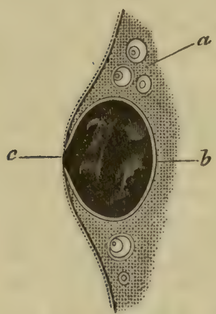
In different species of mammalians, the corpus luteum is characterized by certain peculiarities of size, color, rapidity of growth, and disappearance, which are distinctive for each particular kind of animal; although the general process of its formation and atrophy is the same in all. In the human female it is marked by a moderately large size, a brilliant yellow hue at a certain period of its development, and the presence of blood in its central cavity, distinguishable by its color for two or three weeks after the rupture of the follicle. The details of its growth and retrocession, which follow a certain regular course during the normal recurrence of the menstrual periods, are modified to an appreciable degree by the occurrence of pregnancy. In the first instance, it is known as the *corpus luteum of menstruation;* in the second as the *corpus luteum of pregnancy.*

I. Corpus Luteum of Menstruation.

At each menstrual epoch, in the human female, a Graafian follicle swells, protrudes from the surface of the ovary, ruptures, and discharges its mature egg. At the moment of rupture, or immediately afterward, a somewhat abundant hemorrhage takes place from the follicle, and its cavity is filled with blood. This blood coagulates soon after its exudation, as it would if extravasated elsewhere, and the coagulum is retained in the interior of the Graafian follicle. The opening by which the egg makes its escape is usually a minute rounded perforation, often not more than one millimetre in diameter. A small probe, introduced

through this opening, passes directly into the cavity of the Graafian follicle. If the follicle be opened at this time by a longitudinal incision through the substance of the ovary (Fig. 233), it will be seen to form a globular cavity, between one and two centimetres in diameter, containing a soft, recent, dark-colored coagulum. The coagulum has no organic connection with the walls of the follicle, but lies loose in its cavity, and may be easily turned out with the handle of a knife. There is sometimes a slight mechanical adhesion of the clot to the edges of the lacerated opening; but there is no continuity of substance between them, and the clot may be separated by careful manipulation. The membrane of the vesicle presents at this time a smooth, transparent, and vascular internal surface.

Fig. 233.



Graafian Follicle of the human ovary; recently ruptured during mestruation, and filled with coagulated blood; longitudinal section.—*a.* Tissue of the ovary, containing unruptured Graafian follicles. *b.* Vesicular membrane of the ruptured follicle. *c.* Point of rupture.

An important change soon afterward begins to take place, both in the central coagulum and in the vesicular membrane.

The clot, which is at first large, soft, and gelatinous, begins to contract; and the serum separates from the coagulum proper. The serum, as it separates, is absorbed by the neighboring parts; and the clot, accordingly, grows smaller and denser than before. At the same time the coloring matter of the blood undergoes the usual changes which occur in it after extravasation, and is partially reabsorbed together with the serum. This second change is somewhat less rapid than the former, but a diminution of color is very perceptible in the clot, at the expiration of two weeks from the rupture of the follicle.

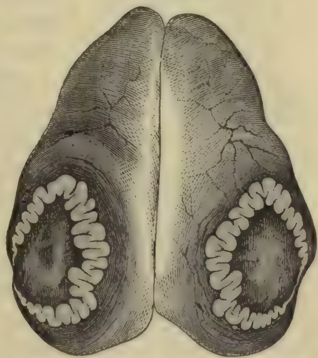
The vesicular membrane during this time is beginning to undergo a process of development, by which it becomes thickened and convoluted, and tends partially to fill the cavity of the follicle. The hypertrophy and convolution of the vesicular membrane commences first and proceeds most rapidly at the deeper part of the follicle, opposite the situation of the rupture. From this point, the membrane becomes thinner and less convoluted as it approaches the surface of the ovary and the edges of the ruptured orifice.

At the end of three weeks, the hypertrophy of the vesicular membrane has reached its maximum. The ruptured Graafian follicle has now become so completely solidified by the growth above described, and by the condensation of its clot, that it presents the appearance of a new body imbedded in the ovarian tissue, and receives the name of *corpus luteum*, although its yellow color is not yet distinctly developed. It forms a perceptible prominence on the surface of the ovary, and may be felt as a well-defined rounded tumor, nearly always somewhat flattened from side to side. It measures about 19 millimetres in length

and about 12 millimetres in depth. On its surface may be seen a minute cicatrix, occupying the spot of the original rupture.

On cutting it open at this time (Fig. 234), the corpus luteum is seen to consist, as above described, of a central coagulum and a convoluted wall. The coagulum is semi-transparent, of a gray or light greenish color, more or less mottled with red. The convoluted wall is about 3 millimetres thick at its deepest part, and of an indefinite yellowish or rosy hue, not very different in tinge from the rest of the ovarian tissue. The convoluted wall and the contained clot lie simply in contact with each other, as at first, without any intervening organic connection; and they may still be readily separated from each other by the handle of a knife or the flattened end of a probe. The whole corpus luteum may also be stripped out, or enucleated from the ovarian tissue, just as might have been done with the Graafian follicle previously to its rupture. When separated in this way from the neighboring parts, it presents itself under the form of a solid globular or flattened mass, with a convoluted external surface covered with the remains of the connective tissue by which it was previously united with the substance of the ovary.

Fig. 234.



HUMAN OVARY cut open, showing a corpus luteum, divided longitudinally; three weeks after menstruation. From a girl, twenty years of age, dead of hæmoptysis.

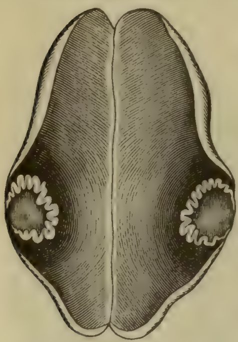
We have had an opportunity of examining a corpus luteum of this period, in an ovary immediately after its removal from the body of the living woman. It was on the occasion of the extirpation by Prof. T. T. Sabine, in 1874, of the left ovary for obstinate ovarian neuralgia, from an unmarried woman, otherwise healthy, 25 years of age.[1] The last menstrual period had terminated exactly three weeks before the date of the operation, and a new one commenced twenty-four hours afterward. The extirpated ovary presented a perfectly normal appearance, and contained a corpus luteum similar in all respects to that represented in Figure 234. Its convoluted wall was fully formed, without any distinctly marked yellow tinge, and the central coagulum was partly, but not entirely, decolorized. The patient recovered without difficulty.

After the third week from the close of menstruation, the corpus luteum passes into a retrograde condition. It diminishes perceptibly in size, and the central coagulum continues to be absorbed and loses still farther its coloring matter. The whole body undergoes a process of partial atrophy; and at the end of the fourth week it is less than 10 millimetres in its longest diameter (Fig. 235). The external cicatrix may still usually be seen, as well as the point where the central coagu-

[1] New York Medical Journal, January, 1875, p. 37.

lum comes in contact with the peritoneal surface. There is still no organic connection between the central coagulum and the convoluted wall; but the partial condensation of the clot and the continued folding of the wall prevent the separation of the two being so easily accomplished as before. The entire corpus luteum may still be extracted from its bed in the ovarian tissue.

Fig. 235.



HUMAN OVARY, showing a corpus luteum, four weeks after menstruation; from a woman dead of apoplexy.

The color of the convoluted wall, during this stage, instead of fading, like that of the fibrinous coagulum, becomes more strongly marked. From having a dull yellowish or rosy hue, as at first, it gradually assumes a more decided yellow. This change of color is produced simultaneously with a kind of fatty degeneration which takes place in its texture; a large quantity of oil-globules being deposited in it at this time, which are recognizable under the microscope. At the end of the fourth week, the alteration in hue is complete; and the outer wall of the corpus luteum is then of a clear chrome yellow color, by which it is readily distinguished from the neighboring tissues.

After this period, the process of degeneration goes on rapidly. The clot becomes more dense and shrivelled, and is converted into a minute, stellate, white, or reddish-white cicatrix. The yellow wall becomes softer and more friable, and shows less distinctly the marking of its convolutions. At the same time its surface becomes confounded with the central coagulum on the one hand, and with the neighboring parts on the other, so that it is no longer possible to separate them fairly from each other. At the end of eight or nine weeks (Fig. 236) the whole mass is reduced to the condition of an insignificant, yellowish, cicatrix-like spot, measuring about 6 millimetres in its longest diameter, in which the original texture of the corpus luteum can be recognized only by the peculiar folding and coloring of its constituent parts. Subsequently its atrophy goes on less rapidly, and a period of seven or eight months sometimes elapses before its complete disappearance.

Fig. 236.

HUMAN OVARY, showing a corpus luteum, nine weeks after menstruation; from a girl dead of tubercular meningitis.

The corpus luteum, accordingly, is a formation which results from the obliteration of a ruptured Graafian follicle. Under ordinary conditions, a corpus luteum is produced at every menstrual period; and notwithstanding the rapidity of its retrogression and atrophy, a new one is always formed before its predecessor has entirely disappeared.

When, therefore, we examine the ovaries of a healthy female, in whom the menses have recurred with regularity for some time previous to death, several corpora lutea will be met with, in different stages of growth. We have found, under such circumstances, four, five, six, and even eight corpora lutea in the ovaries at the same time, perfectly distinguishable by their texture, though very small, and most of them in a state of advanced retrogression. They finally disappear altogether, and the number of those present in the ovary no longer corresponds with that of the Graafian follicles which have been ruptured.

II. Corpus Luteum of Pregnancy.

The process above described takes place at every menstrual period, independently of impregnation and sexual intercourse. The mere presence of a corpus luteum, therefore, is no indication that pregnancy has existed, but only that a Graafian follicle has been ruptured and its contents discharged. It is found, nevertheless, that when pregnancy takes place, the appearance of the corpus luteum becomes so modified as to be readily distinguished from that which follows the ordinary menstrual process.

The distinction between these two kinds of corpora lutea is not an essential or fundamental difference; since they both originate in the same way, and are composed of the same structures. It is only a difference in the rapidity and degree of their development. While the corpus luteum of menstruation passes rapidly through its different stages, and is soon reduced to a condition of atrophy, that of pregnancy continues its development for a longer time, attains a larger size and firmer organization, and disappears at a much later period.

This variation in the history of the corpus luteum depends upon the condition of the pregnant uterus. This organ exerts a sympathetic action, during pregnancy, upon many other parts of the system. The stomach becomes irritable, the appetite is capricious, and even the mental faculties and the moral disposition are frequently more or less affected. The ovaries feel the influence of gestation more decidedly than other organs, since they are more closely connected with the uterus in the ordinary performance of their function. The moment that pregnancy takes place, menstruation is arrested. No more eggs come to maturity, and no more Graafian follicles are ruptured, during the whole period of gestation. It is not surprising that the growth of the corpus luteum should also be modified, by an influence which affects so profoundly the system at large, as well as the ovaries in particular.

During the first three weeks of its formation the growth of the corpus luteum is the same in the impregnated as in the unimpregnated condition. But after that time a difference becomes manifest. Instead of commencing a retrograde course during the fourth week, the corpus luteum of pregnancy continues its development. The external wall grows thicker, and its convolutions more abundant. Its color changes, as

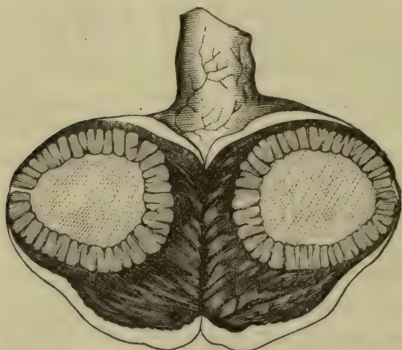
previously described, to a bright yellow; and there is a deposit of fatty matter in the form of microscopic globules.

By the end of the second month, the corpus luteum has so increased in size as to measure 22 millimetres in length by 12 or 13 millimetres in depth (Fig. 237). The central coagulum has by this time become almost entirely decolorized, and presents the appearance of a purely fibrinous deposit. Sometimes it is found that a part of the serum, during its separation from the clot, has accumulated in the centre of the mass, as was the case in Fig. 237, forming a little cavity containing a clear fluid and inclosed by a fibrinous layer, the remains of the solid portion of the clot. The existence of such a cavity, however, is only an occasional, not a constant, phenomenon. More frequently, the fibrinous clot is solid throughout, the serum being gradually absorbed, as it separates spontaneously from the coagulum.

Fig. 237.

Corpus Luteum of pregnancy, at the end of the second month; from a woman dead from induced abortion.

Fig. 238.



Corpus Luteum of pregnancy, at the end of the fourth month; from a woman dead by poison.

During the third and fourth months, the enlargement of the corpus luteum continues; and at the end of that time it may measure 22 millimetres in length by 18 or 19 millimetres in depth. Its flattened form is very manifest, so that, in a longitudinal section, it may present a nearly circular outline, as in Fig. 238, while in a transverse section it is a narrow oval. The convoluted wall is still more highly developed than before, having a thickness, at its deepest part, of nearly 5 millimetres, or double that presented at the same point in the corpus luteum of menstruation, when at its largest size. Its color, however, has already begun to fade, and is of a dull yellowish tinge. The central coagulum, perfectly colorless and fibrinous in appearance, is often so much flattened by the lateral compression of its mass, that it is hardly 2 millimetres in thickness. The other relations between the different parts remain the same.

The corpus luteum has now attained its maximum of development, and continues without any very perceptible alteration during the fifth and sixth months. It then begins to retrograde, diminishing in size during the seventh and eighth months. Its external wall fades still

more, becoming of a faint yellowish-white color, not unlike that presented at the end of the third week. Its texture is thick, soft, and elastic, and it is strongly convoluted. An abundance of fine red vessels can be seen penetrating from the exterior into the interstices of its convolutions. The central coagulum is reduced by this time to the condition of a whitish radiated cicatrix.

Fig. 239.

Corpus Luteum of pregnancy, at term, from a woman dead in delivery from rupture of the uterus.

Its atrophy continues during the ninth month. At the termination of pregnancy, it is reduced in size to 12 or 13 millimetres in length and less than 10 millimetres in depth. (Fig. 239.) It is then of a faint indefinite hue, but little contrasted with the remaining tissues of the ovary. The central cicatrix has become very small, and appears only as a thin whitish lamina, with radiating processes which penetrate between the interstices of the convolutions. The whole mass is still quite firm to the touch, and is readily distinguishable, both from its size and texture, as a prominent feature in the ovarian tissue, and a reliable indication of pregnancy. The convoluted structure of the external wall is very perceptible, and the point of rupture, with its external peritoneal cicatrix, still distinctly visible.

After delivery, the corpus luteum retrogrades rapidly. At the end of eight or nine weeks, it has become so much altered that its color is no longer distinguishable, although indications of its convoluted structure may still be discovered by close examination. These traces of its existence remain for a long time afterward, more or less concealed in the ovarian tissue. We have distinguished them, in one instance, so late as nine and a half months after delivery. They finally disappear entirely, together with the external cicatrix which previously marked their situation.

During the existence of gestation, the process of menstruation being suspended, no new Graafian follicles are ruptured, and no new corpora lutea are produced; and as the old ones, formed before the period of conception, fade and disappear, the corpus luteum which marks the occurrence of pregnancy after a time exists alone in the ovary. In twin pregnancies, we of course find two corpora lutea in the ovaries; but these are precisely similar to each other, and, being evidently of the same date, need not give rise to any confusion. Where there is but a single fœtus in the uterus, and the ovaries contain two corpora lutea of similar appearance, one of them belongs to an embryo which has been blighted in the early part of pregnancy, and has failed of its development. The remains of the blighted embryo may sometimes be discovered, in such cases, in some part of the Fallopian tube, where it has been arrested in its descent toward the uterus.

After lactation has come to an end, the ovaries resume their ordinary function. The Graafian follicles mature and rupture in succession, as before, and new corpora lutea follow each other in alternate development and disappearance.

The corpus luteum of menstruation, therefore, differs from that of pregnancy in the extent of its development and the duration of its existence. While the former passes through all the important phases of its growth and decline in a period of two months, the latter lasts from nine to ten months, and presents, during a great portion of the time, a larger size and a more solid organization. Even in the corpus luteum of pregnancy, the bright yellow color, which is so important a characteristic, is only temporary in duration; not making its appearance till about the end of the fourth week, and again disappearing after the sixth month.

The following table contains, in a condensed form, the characters of the corpus luteum, as belonging to the two different conditions of menstruation and pregnancy, corresponding with different periods of its development.

	Corpus Luteum of Menstruation.	Corpus Luteum of Pregnancy.
At the end of three weeks.	Twelve by nineteen millimetres in diameter; central clot reddish; convoluted wall pale.	
One month.	Smaller; convoluted wall bright yellow; clot still reddish.	Larger; convoluted wall bright yellow; clot still reddish.
Two months.	Reduced to the condition of an insignificant cicatrix.	Twelve by twenty-two millimetres in diameter; convoluted wall bright yellow; clot perfectly decolorized.
Four months.	Absent or unnoticeable.	Eighteen by twenty-two millimetres in diameter; clot pale and fibrinous; convoluted wall dull yellow.
Six months.	Absent.	Still as large as at the end of the second month. Clot fibrinous. Convoluted wall paler.
Nine months.	Absent.	Ten by thirteen millimetres in diameter; central clot converted into a radiating cicatrix; external wall tolerably thick and convoluted, but without any bright yellow color.

CHAPTER VII.

DEVELOPMENT OF THE IMPREGNATED EGG—SEGMENTATION OF THE VITELLUS—BLASTODERM—FORMATION OF ORGANS IN THE FROG.

THE egg, while still contained within the ovarian follicle, passes through a series of consecutive changes, by which it is finally brought to the condition of maturity. During this period it increases in size, from the insignificant dimensions which it presents in the earlier stages of its formation, to those of its complete development as an ovarian egg. The vitellus, at first transparent and colorless, is not only enlarged, but becomes more or less granular and opaque by the deposit of new material in a different form; and in birds and reptiles it assumes a distinctive hue, which is generally orange or yellow. These modifications are due to the spontaneous growth of the egg and the parts in which it is inclosed; and they mark a continuous process of development taking place independently in the generative organs of the female. The last change which occurs in the ovarian egg, and that which indicates its complete maturity, is the disappearance of the germinative vesicle. This body, which is in general a distinctive feature of the ovarian egg, disappears a short time previous to its expulsion, or even when it is just on the point of leaving the Graafian follicle.

The egg, therefore, at the time of its discharge from the ovary, consists solely of the mature vitellus, inclosed in the vitelline membrane; and in this condition it meets with the spermatozoa, usually in some part of the Fallopian tube. By the contact of the male elements, and their union with its own substance, a new stimulus is imparted to its growth; and while, if unimpregnated, its vitality, on arriving at this point, would have reached its termination, the fecundated egg, on the contrary, starts upon a more extensive course of development, by which it is finally converted into the body of the young animal.

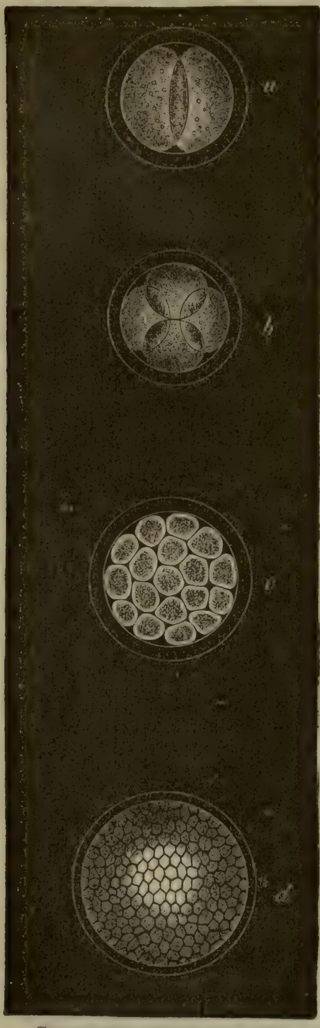
Deposit of Albuminous Layers in the Fallopian Tube.—The egg, in the first place, as it passes down the Fallopian tube, becomes covered with an albuminous secretion. In birds, this secretion is very abundant, and is deposited in successive layers around the vitellus, forming the so-called "white of egg." In reptiles, it is also poured out in considerable quantity, and serves for the nourishment of the egg during its early growth. In mammalians, albuminous matter is supplied in the same way, though in smaller quantity, by the mucous membrane of the Fallopian tube, and envelops the egg in a layer of nutritious material. This albuminous layer, although its absolute quantity is very small, is

sufficiently abundant, in proportion to the size of the mammalian egg; and it serves for the supply of organic material in the earlier stages of development, before the egg has established its connection with the uterine mucous membrane.

Segmentation of the Vitellus.—A very important change now takes place in the impregnated egg, which is known as the division, or *segmentation*, of the vitellus. A furrow shows itself, running round the globular mass of the vitellus in a vertical direction, which gradually deepens until it has divided the vitellus into two separate halves or hemispheres (Fig. 240, *a.*) Almost at the same time another furrow, running at right angles with the first, penetrates the substance of the vitellus, and cuts it in a transverse direction. The vitellus is thus divided into four equal portions (Fig. 240, *b*), the edges and angles of which are rounded off, and which are still contained in the cavity of the vitelline membrane. The spaces between them and the internal surface of the vitelline membrane are occupied by a transparent fluid.

The process thus commenced goes on by a successive formation of furrows and sections, in various directions. The four vitelline segments already produced are subdivided into sixteen, the sixteen into sixty-four, and so on; until the whole vitellus is converted into a mulberry-shaped mass of minute, nearly spherical bodies, called the "vitelline spheres." (Fig. 240, *c.*) The vitelline spheres have a somewhat firmer consistency than the original substance of the vitellus; and this consistency appears to increase as they multiply in numbers and diminish in size. At last they become so abundant as to be closely crowded together and compressed into polygonal forms. (Fig. 240, *d.*) They have by this time been converted into a layer of cells, surrounding the original central cavity of the egg, and themselves enveloped by the vitelline membrane.

Fig. 240.



SEGMENTATION OF THE VITELLUS.

The segmentation of the vitellus constitutes the primary act in the development of the impregnated egg. It is this remarkable process which is the sign that fecundation has taken place, and that the forma-

tion of an embryo has commenced. It takes place in all species of animals, although it varies in detail according to the special constitution of the egg, and the presence or absence of accessory parts. In all the mammalia, as well as in many of the invertebrates, where the vitellus is very small, and where the body of the embryo immediately after its formation is to be supplied with nourishment from without, the process is that described above. In the birds, in scaly reptiles, and in many fish, where the vitellus or yolk is of large size, and contains additional nutritive matter, segmentation takes place only in a thin layer which occupies the surface of the great mass of the yolk; and, beginning at one spot, extends thence from within outward, so that it advances more rapidly at the centre of the segmenting region than at its periphery. But in all cases segmentation of the vitellus is the first change to occur in the process of development, and its result is always the same, namely, to divide the vitellus, which was at first of uniform texture throughout, into a great number of minute bodies, which soon present the character of animal cells.

Blastoderm, or Germinal Membrane.—The cells which are formed, in the manner above described, by the segmentation of the vitellus, become more closely packed as they increase in number; and finally, by their mutual contact, and adhesion at their adjacent edges, they serve to form a continuous organized membrane, known as the germinal membrane or *blastoderm.*

During the formation of this membrane, moreover, the egg, while passing through the Fallopian tube, increases in size. The albuminous matter with which it is enveloped becomes liquefied; and, being absorbed by endosmosis through the vitelline membrane, furnishes the material for the more solid and extensive growth of the newly-formed structures. A certain quantity of fluid also accumulates in the central cavity of the egg.

The next change which takes place consists in the division or splitting of the blastoderm into two layers, which are known as the *external* and *internal blastodermic layers.* They are both still composed exclusively of cells; but those of the external layer are smaller and more compact, while those of the internal are larger and less consistent. The egg then has the form of a globular sac, the walls of which consist of three concentric layers, lying in contact with and inclosing each other, namely: 1st, the structureless vitelline membrane on the outside; 2d, the external blastodermic layer, composed of cells; and 3d, the internal blastodermic layer, also composed of cells. The cavity of the egg is occupied by an albuminous fluid, absorbed from the exterior and destined to serve as nutritious material.

It is by this process that the simple globular mass of the vitellus is converted into an organized structure. For the blastoderm, although consisting only of cells which are nearly uniform in size and shape, is nevertheless an organized membrane, made up of anatomical elements. It is the first sign of distinct organization which makes its appearance

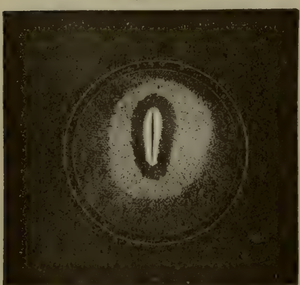
in the egg; and as soon as it is completed, the body of the fœtus is formed. The blastoderm is, in fact, the fœtus in its earliest condition; for although its texture is at this time exceedingly simple, all the various organs of the body will afterward be produced from it by the modification of its different parts. The further process of formation is comparatively simple in some classes of animals, more complicated in others; and its general features are most easily understood by commencing with the study of embryonic development as it takes place in the frog.

Formation of Organs in the Embryo.—The egg of the frog, when discharged and fecundated, is deposited in the water, enveloped in an elastic cushion of albuminous matter. It is thus freely exposed to the light, the air, and the moderate warmth of the sun's rays, and is supplied with an abundance of moisture and appropriate nutritious material. Its development is distinguished accordingly by a character of great simplicity; since the whole of the vitellus is directly converted into the body of the embryo. There are no accessory organs required, and consequently no complications of the formative process.

The two blastodermic layers, above described, represent together the commencement of the body of the embryo. They serve, however, for the production of two different systems; and the entire process of their development may be expressed as follows: *The external blastodermic layer produces the skin, the cerebro-spinal axis, and the organs of animal life; while the internal layer produces the mucous membrane of the alimentary canal, and the organs of nutrition.*

The first sign of advancing organization in the external blastodermic layer shows itself in a thickening and condensation of its structure. The thickened portion has the form of an elongated oval spot, termed the "embryonic spot" (Fig. 241), the wide edges of which are somewhat more opaque than the rest of the blastoderm. Inclosed within these opaque edges is a narrower colorless and transparent space, the "area pellucida," and in its centre is a delicate line, or furrow, running longitudinally from front to rear, called the "primitive trace."

Fig. 241.



Diagrammatic view of the IMPREGNATED EGG, showing the embryonic spot, area pellucida, and primitive trace.

In the anterior portion of the area pellucida, the substance of the blastoderm rises up in such a manner as to form two nearly parallel ridges or plates, which approach each other, from side to side, over what will be the dorsal aspect of the embryo, and are therefore called the "dorsal plates." Between them is included a groove, termed the "medullary groove." The dorsal plates gradually meet each other and coalesce upon the median line, thus converting the intervening groove into a canal. The coalescence of the edges of the two dorsal plates takes place first in the

anterior part of the area pellucida and extends gradually backward; and when it is complete throughout their length, the whole of the medullary groove has been converted into a closed canal. This is the "medullary canal;" and in its cavity will afterward be formed the cerebro-spinal axis, by a growth of nervous matter from its internal surface. At its anterior extremity, the medullary canal is large and rounded, to accommodate the brain and the medulla oblongata; its remainder is narrow, and pointed posteriorly, and is destined to contain the spinal cord.

In a diagrammatic section of the egg at this stage, made transversely to the longitudinal axis of the embryo (Fig. 242), the dorsal plates may be seen approaching each other above, on each side of the medullary groove. At a more advanced period (Fig. 243) they are fairly united with each other, and inclose the cavity of the medullary canal. At

Fig. 242.

Diagrammatic section of the impregnated EGG in an early stage of development.—1. External blastodermic layer. 2, 2. Dorsal plates. 3. Internal blastodermic layer.

Fig. 243.

IMPREGNATED EGG, at a somewhat more advanced period.—1. Point of union between the abdominal plates. 2, 2. Dorsal plates united with each other on the median line and inclosing the medullary canal. 3, 3. Abdominal plates. 4. Section of the spinal column, with laminæ and ribs. 5. Internal blastodermic layer.

the same time, the edges of the thickened portion of the blastoderm grow outward and downward, extending over the lateral portions of the vitelline mass. These are called the "abdominal plates;" and, as they enlarge, they tend to approach each other below and inclose the abdominal cavity, as the dorsal plates united above, and inclosed the medullary canal. At last the abdominal plates actually unite on the median line (at 1, Fig. 243), embracing the whole of the internal blastodermic layer (5), which incloses in turn the remains of the original vitellus and the albuminous fluid accumulated in its cavity.

During this time, there is formed, in the thickened central part of the blastoderm, immediately beneath the medullary canal, a longitudinal cartilaginous cord, the "chorda dorsalis." Around the chorda dorsalis

are afterward developed the bodies of the vertebræ (Fig. 243, 4), and the oblique processes of the vertebræ run upward from this point into the dorsal plates, while the transverse processes and ribs run outward and downward in the abdominal plates, to encircle more or less completely the corresponding portion of the body.

In a longitudinal section of the egg, made while this process is going on, the thickened portion of the external blastodermic layer (Fig. 244, 1) may be seen in profile. The anterior portion (2), which will form the head, is thicker than the posterior (3), which will form the tail. As the whole mass grows rapidly, both in the anterior and the posterior direction, the head becomes thick and voluminous, while the tail begins to project backward, and the egg assumes an elongated form. (Fig. 245.)

Fig. 244.

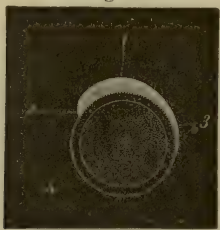


Diagram of FROG'S EGG, in an early stage of development; longitudinal section.—1. Thickened portion of external blastodermic layer. 2. Anterior extremity of the embryo. 3. Posterior extremity. 4. Internal blastodermic layer. 5. Cavity of vitellus.

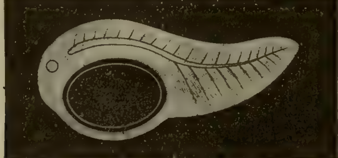
Fig. 245.

EGG OF FROG, in process of development.

The abdominal plates also meet upon its under surface, and complete the closure of the abdominal cavity. The internal blastodermic layer is seen, in the longitudinal section of the egg, embraced by the abdominal plates, and inclosing, as before, the remains of the vitellus.

As development goes on (Fig. 246), the head becomes larger, and shows traces of the formation of organs of special sense. The tail also

Fig. 246.



EGG OF FROG, farther advanced.

increases in size, and projects farther from the posterior extremity of the embryo. The spinal cord runs in a longitudinal direction from front to rear, and its anterior extremity enlarges, to form the brain and medulla oblongata. In the mean time, the internal blastodermic layer, which is subsequently converted into the intestinal canal, has been shut

in by the abdominal walls, and still forms a closed sac, of slightly elongated figure, without inlet or outlet. Afterward, the mouth is formed by means of a perforation, which takes place through both external and internal layers at the anterior extremity; while a similar perforation, at the posterior extremity, results in the formation of the anus.

By a continuation of the same process, the different portions of the external blastodermic layer are further developed, resulting in the complete formation of the various parts of the skeleton, the integument, the organs of special sense, and the voluntary muscles and nerves. The tail at the same time acquires sufficient size and strength to be capable of acting as an organ of locomotion. (Fig. 247.) The intestinal canal,

Fig. 247.

TADPOLE, fully developed.

which has been formed from the internal blastodermic layer, is at first a short, wide, and nearly straight tube, running directly from the mouth to the anus. It soon, however, begins to grow faster than the abdominal cavity which incloses it, becoming longer and narrower, and is at the same time thrown into numerous curvilinear folds.

Arrived at this period, the young tadpole ruptures the vitelline membrane, by which he has heretofore been inclosed, and leaves the cavity of the egg. He at first fastens himself upon the remains of the albuminous matter deposited round the egg, and feeds upon it for a short period. He soon, however, acquires sufficient strength and activity to swim about freely in search of other food, propelling himself by means of his large, membranous, and muscular tail. The alimentary canal increases in length and becomes spirally coiled up in the abdominal cavity, attaining a length from seven to eight times greater than that of the entire body.

After a time, a change takes place in the external form of the animal. The posterior limbs are the first to make their appearance, by budding or sprouting from the sides of the body at the base of the tail. (Fig. 248.) The anterior extremities are for a time concealed beneath the integument, but afterward become liberated, and show themselves externally. At first both the fore and hind legs are very small, incomplete in structure, and useless for purposes of locomotion. They soon, however, increase in size and strength; while the tail, on the contrary, ceases to grow, and becomes shrivelled and atrophied. The limbs, in fact, are destined finally to replace the tail as organs of locomotion; and

a time at last arrives (Fig. 249) when the tail has altogether disappeared, while the legs have become fully developed, muscular, and powerful. Then the animal, heretofore confined to an aquatic mode of life, becomes capable of living upon land, and a transformation is effected from the tadpole into the frog.

Fig. 248.

TADPOLE, with limbs beginning to be formed.

Fig. 249.

Perfect FROG.

During the same time, other changes of equal importance take place in the internal organs. The tadpole at first breathes by gills; but these organs subsequently become atrophied, and are replaced by lungs. The structure of the mouth, also, of the integument, and of the circulatory system, is altered to correspond with the varying conditions and wants of the growing organism; and all these changes taking place, in part successively and in part simultaneously, bring the animal at last to a state of complete formation.

The process of development, as thus far described, may be recapitulated as follows:

1. The germinal membrane or blastoderm, produced by the segmentation of the vitellus, consists of two cellular layers, namely, an external and an internal blastodermic layer.

2. The external blastodermic layer incloses by its dorsal plates the cerebro-spinal canal, and by its abdominal plates the abdominal or visceral cavity.

3. The internal blastodermic layer forms the intestinal canal, which becomes lengthened and convoluted, and communicates with the exterior by a mouth and anus of secondary formation.

4. Finally, the cerebro-spinal axis and its nerves, the skeleton, the organs of special sense, the integument, and the voluntary muscles, are developed from the external blastodermic layer; while the anterior and posterior extremities are formed from the same layer by a process of sprouting, or continuous growth.

CHAPTER VIII.

FORMATION OF THE EMBRYO IN THE FOWL'S EGG.

In the preceding chapter a condensed description has been given of the general phenomena of embryonic development, as illustrated in the egg of the frog. This species is useful as an example, to exhibit the progressive alterations of form which lead to the final production of a vertebrate animal out of the fecundated vitellus, uncomplicated by the presence of any accessory organs. But the development of the chick, in the egg of the fowl during incubation, has been found more favorable for the study of certain important details. The readiness with which the fowl's egg may be obtained in all the successive stages of incubation, and the convenient size of the embryo in the earlier periods of its formation, have made it a favorite subject of investigation for embryologists; and some of the most valuable discoveries in this department of physiology have resulted from observations upon the young chick and the mode of formation of its different organs.

The Yolk and the Cicatricula.—The yolk of the fowl's egg represents something more than the vitellus proper. Its principal mass consists of an opaque, yellow, semifluid substance, the "yellow yolk," which solidifies on boiling, owing to its large proportion of albuminous matter. This substance contains a great abundance of soft, spherical, finely granular bodies, from 25 to 100 mmm. in diameter.

The yellow yolk is surrounded everywhere by a thin layer of nearly colorless appearance, the "white yolk," which contains, instead of the granular spheres described above, smaller globular bodies with one or more brightly refracting masses in their interior. The albuminous matter of the white yolk, furthermore, does not solidify firmly on the application of heat; so that in a boiled egg the thin outer stratum of this substance remains semifluid. There is also a spot in the centre of the yolk-sphere, which is occupied by the same material, and which consequently remains soft in the boiled egg; the central cavity thus left communicating with the surface of the yolk by a narrow passage, like the neck of a flask.

The whole yolk is thus formed of two substances, which are distinguished from each other by their microscopic characters and by their comparative coagulability at the temperature of boiling water. Neither of the two corresponds with the granular vitellus of the mammalian egg; and the yolk, as a whole, constitutes a deposit of nutritious material, superadded to the vitellus proper, and destined to be absorbed for the support of the embryonic tissues. This yolk, however, is formed, in

birds, within the ovarian follicle, and is, in respect to its volume, the main constituent of the ovarian egg.

At one point upon the surface of the yolk of the fowl's egg, while still contained within the ovarian follicle, there is a whitish circular spot about 5 millimetres in diameter, lying immediately beneath the vitelline membrane. This is the *cicatricula.* It is a thin layer of uniformly granular material, containing none of the spherical bodies found in the white and yellow yolk. Its granules are imbedded in a homogeneous substance of viscid consistency, by which they are agglutinated into a disk-like mass. In its centre is contained the germinative vesicle, which is distinctly visible by its transparency and well-defined outline, until the mature egg is ready to leave the ovary, when it disappears, as in other classes of animals. The cicatricula of the fowl's egg corresponds, therefore, in its structure, though not in its form, with the entire vitellus of the mammalian egg. Its position is always exactly above the tubular prolongation of white yolk, already described as leading to the central cavity of the egg.

Formation of the Blastoderm.—The fowl's egg is fecundated soon after leaving the ovary, and while in the upper portion of the oviduct. The segmentation of the cicatricula then begins, by a furrow which passes across its disk, and which is followed by others running in different directions. By the continued multiplication of these furrows, the substance of the cicatricula is divided successively into smaller and smaller portions; the process beginning and proceeding most rapidly at its centre, but extending thence outward to the periphery. When these divisions have become reduced in size and increased in number to a certain degree, they present, as in other instances, the form and structure of distinct cells. The cells are in two layers. Those of the upper layer are smaller, more numerous, cylindrical or prismatic

Fig. 250.

VERTICAL SECTION THROUGH A PORTION OF THE BLASTODERM of a fowl's egg, at the commencement of incubation.—1. Upper cellular layer. 2. Lower cellular layer. 3, 3. Larger cells, found in small number beneath those of the lower layer. (Foster and Balfour.)

in form, standing upright side by side, like the cells of columnar epithelium, and adherent to each other by their adjacent surfaces. According to Foster and Balfour[1] they have a very uniform size of 9 mmm., and most, if not all of them are provided with a distinct oval nucleus. The

[1] Elements of Embryology. London, 1874, p. 17.

cells of the lower layer are rather larger, more globular in form, and less closely united with each other. The whole forms an organized cellular membrane, the *blastoderm*, which occupies the place of the original cicatricula.

Thus the blastoderm, or germinal membrane, is formed in the impregnated fowl's egg by a process of segmentation essentially similar to that which takes place in eggs of other kinds. It presents the appearance of a thin sheet, of uniform texture, composed of nothing but cells, lying at one spot upon the surface of the yolk. Its formation, which begins immediately after the impregnation of the egg, continues, under the influence of the animal temperature, during the eighteen or twenty hours that the egg is retained in the oviduct for the deposit of its albumen and external envelopes. According to Foster and Balfour, it has reached the condition of a distinct cellular membrane at the time of the expulsion of the egg. If afterward kept at a low temperature it remains in this state; but, if subjected to natural or artificial incubation at a temperature of 38° (100° F.), it goes on to the further development of the body of the embryo.

Folds of the Blastoderm.—The form of the body of the embryo and of its different parts is sketched out, in all cases, by means of a series of folds, which show themselves at various points in the blastoderm. This membrane presents at first a flat surface; or, if it have a certain degree of convexity, corresponding with that of the yolk upon which it lies, this convexity is perfectly uniform, and is too slightly pronounced to be appreciable within the limits of the blastoderm. But as soon as development begins to make a definite progress, this uniformity of surface is broken by the appearance of folds or ridges, which are directed longitudinally or transversely, and which thus mark the lines of separation between different parts of the blastoderm. Such a fold, running in a curvilinear direction from side to side, marks the position of the head of the embryo, and is called the "head-fold." The free border of this mass, projecting forward and above the neighboring portion of the blastoderm, becomes in fact the head, which, as well as the neck, is curved more and more forward and downward, in the subsequent stages of embryonic growth, with the deepening of the fold which first gave origin to it as a distinct part. A similar transverse curvilinear fold at the posterior portion of the area pellucida, marks off the hinder extremity of the embryo, and is called the "tail-fold." Longitudinal folds are also formed in the same manner, one on each side, which fix the lateral limits of the body of the embryo.

By this means, a certain portion of the blastoderm becomes distinctly marked off from the rest. The part included within the transverse and longitudinal folds is immediately recognizable as the body of the embryo; while that which remains outside these limits becomes developed into accessory organs, playing an important though secondary part in the history of development. This forms a marked distinction between the process as it takes place in the fowl's egg, and that already described in

the egg of the frog. In the frog, the whole of the blastoderm serves for the formation of the body of the embryo. In the fowl, only a portion of it is immediately devoted to that object; while the remainder extends itself over the voluminous yolk, to be employed for the absorption of nutritious material and its indirect transfer to the embryonic tissues.

But even within the limits of the body of the embryo, similar folds of the blastoderm become visible, and are the principal means of formation for its different organs. The earliest permanent appearances of this kind are the longitudinal ridges which include between them the "medullary groove" (Fig. 252, I.), and which afterward, by coalescing with each other along the median line of the back, inclose the medullary canal (Fig. 252, II.). That these ridges or "dorsal plates," as well as the groove between them, are produced by the formation of folds, is plain from the fact that the surface of the groove, while still open, is continuous, over its undulating borders, with that of the neighboring part of the blastoderm; and that after its closure, its cavity is lined with a layer of cells identical in form with those on the free surface of the blastoderm above. It is also shown, by transverse sections of the embryo (His, Foster and Balfour), that the folds in question pass through the whole thickness of the outer blastodermic layer. According to Foster and Balfour, the medullary canal, in the fowl's egg, is completely closed at the region of the head on the second day of incubation; after which the coalescence of its edges goes on progressively from before backward.

The closure of the abdomen in front, and the conversion of the inner layer of the blastoderm into an intestinal canal, take place by a similar production of lateral folds, approaching each other along the median line. For, as the limits of the body of the embryo are marked off, on each side, from the rest of the blastoderm by an inverted fold, when this fold becomes deeper its borders are brought nearer to each other. Thus the body of the embryo is at first spread out on the surface of the vitellus, lying, as it were, upon the mucous membrane of its open alimentary canal. But as the folds which mark its lateral borders penetrate more deeply below the surface (Fig. 252, IV.), the sides of the embryo shut in between them a portion of this mucous membrane, and at last completely inclose it in the abdominal cavity, in the same manner as the dorsal folds inclose the medullary canal.

The folds of the blastoderm, which thus determine the configuration of the embryo, are the result of a special activity of growth in particular parts of the blastodermic layers. If the blastoderm were to grow only at its edges, these would simply extend farther and farther over the vitellus, the central portion remaining as before. Or if it were to increase at a uniform rate in all its parts at the same time, its form would not necessarily be subjected to any special alteration. This is what really takes place during the production of the blastoderm itself. The segmentation of the vitellus, and the organization of the cellular layers, go on with a similar activity in all directions, extending uni-

formly from the centre outward. The blastoderm accordingly, when completed, is a smooth, even membrane, having the same texture throughout.

But when the process of incubation commences, the blastoderm grows more rapidly at particular points, and along certain lines of direction, than elsewhere. What may be the determining cause of such a concentration of growth in special situations, it is impossible to say; but its result is that the blastoderm, enlarging more rapidly in one direction than another, is thrown into undulations, which indicate, by their position and size, the unequal expansion of the blastodermic membrane. Thus, if it grow more rapidly at one particular point than in any of the surrounding parts, it will form at that spot a conical eminence or depression, according as it meets with less resistance above or below. If a similar rapidity of increase were to affect a considerable portion of the membrane along a transverse line, the consequence would be a transverse fold; and if the same thing were to occur in an antero-posterior direction, it would cause a longitudinal fold. The subsequent history of embryonic development shows continual repetitions of this process, often on a much larger scale than that exhibited in the blastoderm. The folds of the intestinal canal, the valvulæ conniventes of its mucous membrane, the convolutions of the brain, and the tubular windings of the perspiratory glands, with many other analogous forms, are produced in a similar way. All these structures are at first smooth or straight. They become thrown into folds or convolutions at some period during the development of the embryo, whenever they grow more rapidly than the surrounding parts.

Position of the Embryo in the Egg.—Although the blastoderm is at first apparently of uniform structure throughout, yet each particular part has from the beginning a physiological individuality, which leads to its subsequent development into a special organ or part of an organ. This is evident from the manner in which the local activity of nutrition gives rise to the appearance of folds, running in definite directions, and determining in this way the future location of the head, the tail, and the sides of the body. But it is manifested still more remarkably in the position assumed by the entire embryo. The yolk of the fowl's egg has a nearly regular spherical form; and the cicatricula, as well as the blastoderm into which it is converted, is a circular spot upon its surface. The ovoid form presented by the whole egg, with one round and one pointed extremity, is given to it by the deposit of albumen round the yolk, in the middle and lower parts of the oviduct, after fecundation has taken place. And yet, when the rudiments of the embryo first become peceptible in the area pellucida, it is so placed as to lie crosswise to the long axis of the egg, with its right side toward the round end and its left side toward the pointed end. The exceptions to this rule are so few as to show that, even before incubation has commenced, one particular portion of the circular blastoderm is destined to become

the head and another portion the tail; and consequently that every one of the future organs of the embryo has its point of origin already fixed.

Division of the Blastodermic Layers.—The blastoderm when first formed consists, as above described, of two layers of cells; those of the external layer being cylindrical and compact, those of the internal, larger, rounded, and more loosely connected. The outer blastodermic layer forms the tegumentary surface of the body and the cavity of the cerebro-spinal axis; the inner is converted into the mucous membrane of the alimentary canal. But between the two there soon appears another formation of cells, which is sometimes spoken of as the third or "intermediate" blastodermic layer. The cells of this layer are in immediate contact with, and more or less adherent to, those of the two others; but they are rounded in form and rather loosely united, in comparison both with those above and below. The intermediate layer, in the blastoderm of the fowl's egg, is distinctly formed, according to Foster and Balfour, in the first twelve hours of incubation.

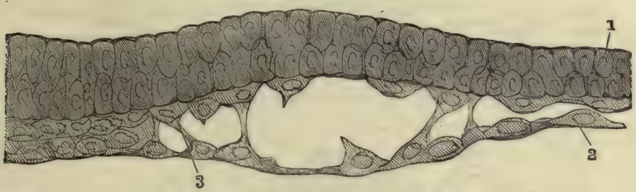
The exact number and designation of the fundamental layers of the blastoderm has been and still is the main point of discrepancy in the writings of embryologists. There is no difference of opinion as to the existence or destination of the two principal layers, namely, the external and internal, which are the first to make their appearance, as above described. They form respectively the basis for the production of the external sensitive integument and cerebro-spinal axis on the one hand, and for the lining of the alimentary canal with its adjacent glandular organs on the other. But the intermediate portion, formerly described as the "vascular layer," is connected both with the organs of animal life and with those of digestion and nutrition. It is, therefore, by some regarded as an independent layer, equal in original importance to the other two; by others as an accessory formation, destined to aid in the development of both the external and internal parts. According to His,[1] whose observations are among the most extensive and valuable in the department of embryology, the most appropriate enumeration is the older one, of an external and internal blastodermic layer; since the cells of the intermediate portion remain attached partly to the outer and partly to the inner layer, when the separation between the two takes place in the manner now to be described.

Immediately underneath the medullary canal, along the axial line of the body of the embryo, there is formed in the intermediate layer of the blastoderm a cylindrical cord, termed the "chorda dorsalis" (Fig. 252, 6), which marks the situation of the future spinal column. For a certain distance on each side of the chorda dorsalis, the component parts of the blastoderm remain in contact with each other throughout its thickness. But farther outward, toward the edges of the embryo, it separates, by a horizontal division or cleavage, into two laminæ, an outer and inner, or upper and lower. This cleavage takes place appa-

[1] Unsere Körperform. Leipzig, 1875, p. 38.

rently in consequence of an unequal rapidity of growth in the two blastodermic layers. Bóth layers are now extending outward, downward, and inward, by the deepening of the lateral longitudinal folds; tending to approach the median line and thus shut in the abdomen and alimentary canal. But the external layer, which is to form the walls of the abdomen, grows more rapidly, and tends to inclose a larger space, than the internal layer, which is to form the lining membrane of the intestine. Wherever this happens, a separation takes place between the two, at the expense of the intermediate layer, some of the cells of which remain attached to the external and some to the internal blastodermic layer.

Fig. 251.



VERTICAL SECTION OF A PORTION OF THE BLASTODERM OF THE FOWL'S EGG, in process of separation into two laminæ.—1. External blastodermic layer. 2. Internal blastodermic layer. 3. Cells of the intermediate layer, partly drawn out into filamentous extensions. Magnified 250 diameters. (His.)

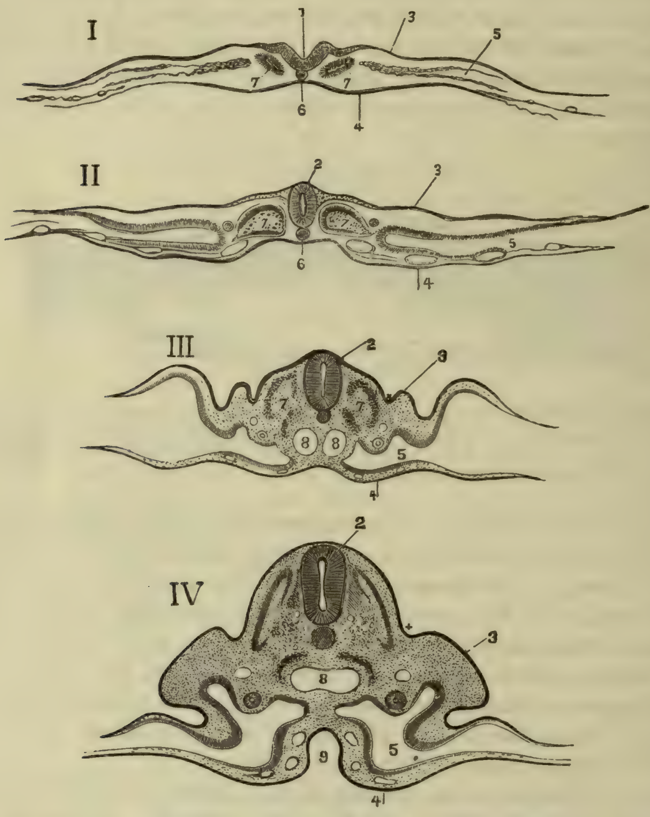
The cleavage or division of the blastoderm into two laminæ, as above described, does not take place everywhere simultaneously. It occurs here and there, as the process of growth becomes more active in particular spots. But the general course of its extension is from without inward, or from the lateral borders of the embryo toward the median line. It does not, however, reach the median line, but leaves a considerable space around the chorda dorsalis and on each side of it still undivided, when the lateral portions of the blastoderm are already completely separated into their two laminæ.

By the separation of the laminæ of the blastoderm thus effected, a space or interval (Fig. 252, 5) is left between the two. This space, when the closure of the abdominal walls is accomplished, becomes the peritoneal cavity. The cells of the intermediate layer subsequently give rise to the development of muscular tissue; and that portion which, in the separation of the two laminæ, continues adherent to the external layer, produces the voluntary muscles of the chest and abdomen. The portion remaining adherent to the internal layer, on the other hand, produces the involuntary muscular coat of the alimentary canal. In Figure 252, II., III., and IV., these two portions of the intermediate layer, which give rise respectively to voluntary and involuntary muscular tissue, are seen shaded with parallel lines.

Primitive Vertebræ—Formation of the Spinal Column and its Muscles.—Already on the second day of incubation there have appeared, on each side of the chorda dorsalis and medullary canal, a number

of rectangular masses arranged in longitudinal series, almost exactly similar to each other, and separated by regular transverse divisions. They resemble strongly in their appearance the simpler component parts of a spinal column, and, in fact, form the basis out of which this struc-

Fig. 252.



TRANSVERSE SECTION OF THE CHICK-EMBRYO, at different stages of development. Magnified 40 diameters.

I. On the second day of incubation.
II. Between the second and third days.
III. On the third day.
IV. On the fourth day.

1. Medullary groove. 2. Medullary canal. 3. External blastodermic layer. 4. Internal blastodermic layer. 5. Space of separation between the two laminæ of the blastoderm; future peritoneal cavity. 6. Chorda dorsalis. 7. Primitive vertebræ. 8. Aorta. 9. Cavity of the intestine. (His.)

ture will afterward be developed. But they do not represent immediately and exclusively the bodies of the vertebræ. They are to serve, not only for the formation of these organs, but also for that of the spinal muscles on the one hand and of the muscular layer of the aorta on the other. They are therefore known as the *primitive vertebræ*. In a transverse section of these bodies (Fig. 252, 7) there is an evident dis-

tinction between their central portion or nucleus, and their external portion or shell. The nucleus is more transparent, and will afterward supply the cartilaginous deposit for the permanent vertebræ; the shell has a radiating striated texture, and serves for the formation of muscular tissue.

On the second day of incubation (Fig. 252, I.) the primitive vertebræ, as seen in transverse section, have the form of a narrow oval, with a small nucleus and a comparatively thick and perfectly continuous shell. From the second to the third day (Fig. 252, II.) the nucleus grows more rapidly than the outer parts, which it pushes upward and downward; and the shell begins to show indications of a separation into upper and lower portions. On the third day (Fig. 252, III.) this separation is complete; and the upper portion of the shell, taking a position more or less parallel with the outline of the body at this point, will become the layer of voluntary muscles about the spinal column. Its lower portion recedes farther from above downward, and approaches the situation of the double aorta (8), which it will afterward supply with its involuntary muscular layer. In a section of the embryo at the fourth day (Fig. 252, IV.) the final position of these two muscular layers is distinctly marked; the projection of the spinal ridge, on the one hand, having become higher and steeper, and, on the other, the double aorta having been fused into a single vascular canal.

The nucleus of the primitive vertebra, in the mean time, extends upward and inward, in such a manner as to surround both the medullary canal and the chorda dorsalis, which it embraces in a tissue of new formation. This tissue afterward supplies the cartilage, both of the bodies of the vertebræ, and of the oblique processes which inclose the spinal canal at its sides and behind. But when these cartilages are formed, it is observed that they do not correspond in situation with the original primitive vertebræ. A new segmentation takes place, by which the lines of separation between the successive permanent vertebræ pass through the middle of what were the primitive vertebræ;[1] and consequently each permanent vertebra is formed out of the adjacent halves of two primitive vertebræ. The chorda dorsalis, included in the cartilaginous matrix of the bodies of the vertebræ, ceases to grow in a corresponding ratio with the neighboring parts, becomes atrophied, and disappears; while the bodies of the vertebræ, which surround it, are rapidly enlarged, and assume the form and size of the principal component parts of the spinal column.

[1] Foster and Balfour, Elements of Embryology. London, 1874, p. 153.

CHAPTER IX.

DEVELOPMENT OF ACCESSORY ORGANS IN THE IMPREGNATED EGG. UMBILICAL VESICLE, AMNION, AND ALLANTOIS.

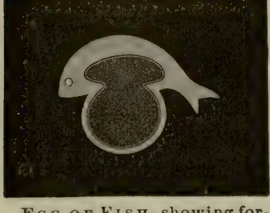
Thus far, the process of development has been followed as it relates to the primary formation of the principal parts of the body of the embryo. In some species of animals this includes all the important structures which show themselves in the impregnated egg; the embryo arriving very soon at a stage of growth in which it is liberated by the rupture of the vitelline membrane and is already capable of carrying on an independent existence. But in many fish and reptiles, and in all birds and mammalia, there are additional structures which aid in the nutrition of the young animal during the middle and later periods of its development. In these instances, the whole of the blastoderm is not immediately converted into the tissues of the embryo. Certain portions, both of its external and internal layers, remain outside the limits of the body, and perform, in this situation, the function of accessory organs. These organs are the umbilical vesicle, the amnion, and the allantois.

Umbilical Vesicle.

In the frog's embryo (page 725), the abdominal plates, closing together in front, join each other upon the median line, and shut in directly the whole of the vitellus, which is thus inclosed in the intestinal sac formed by the internal blastodermic layer.

In other instances, the abdominal plates do not immediately embrace the whole of the vitelline mass, but tend to close together at some intermediate point; so that the vitellus is constricted, and divided into two portions, one internal, and one external. (Fig. 253.) As development proceeds, the body of the embryo increases in size out of proportion to the vitelline sac, and the constriction just mentioned becomes at the same time more strongly marked; so that the separation between the internal and external portions of the vitelline sac is nearly complete. The internal blastodermic layer is by this means divided into two portions, one of which forms the intestinal canal, while the other, remaining outside, forms a sac-like appendage to the abdomen, known by the name of the *umbilical vesicle.*

Fig. 253.



Egg of Fish, showing formation of umbilical vesicle.

The umbilical vesicle is accordingly lined by a portion of the internal blastodermic layer, continuous with the mucous membrane of the intestine; and covered by a portion of the external blastodermic layer, continuous with the integument of the abdomen.

After the young animal leaves the egg, the umbilical vesicle in some species becomes shrunken and atrophied by the absorption of its contents; while in others, the abdominal walls gradually extend over it, and crowd it back into the abdomen; the nutritious matter which it contains passing from the cavity of the vesicle into that of the intestine by the narrow passage remaining open between them.

In the human species, on the other hand, as well as in quadrupeds, the umbilical vesicle becomes more completely separated from the abdomen. There is at first a wide communication between the cavity of the umbilical vesicle and that of the intestine; subsequently this communication is gradually narrowed by the constriction of the abdominal walls; and this constriction proceeds so far that the opposite surfaces of the canal at least come in contact with each other and adhere together, so that the passage previously existing, between the cavity of the intestine and that of the umbilical vesicle, is obliterated, and the vesicle is then connected with the abdomen only by an impervious cord. This cord afterward elongates, and becomes converted into a slender pedicle (Fig. 254), emerging from the abdomen of the fœtus, and connected by its farther extremity with the umbilical vesicle, which is filled with a transparent, colorless fluid. The umbilical vesicle is distinctly visible in the human fœtus so late as the end of the third month. After that period it diminishes in size, and is gradually lost in the advancing development of the neighboring parts.

Fig. 254.

HUMAN EMBRYO, with umbilical vesicle; about the fifth week.

Amnion and Allantois.

The amnion and allantois are two organs which can be best studied in connection with each other, since they are closely related in physiological importance; the office of the first being to provide for the formation of the second. The amnion is developed from the external blastodermic layer; the allantois from the internal layer. The amnion is so called probably from the Greek ἀμνίς, a young lamb; on account of its having been first observed as a fœtal envelope in this animal. The name of the allantois is also derived from the Greek ἀλλαντοειδής, owing to its elongated or sausage-like form in the pig, and some other of the domestic animals.

In the frog's egg, the embryo is abundantly supplied with moisture, air, and nourishment from without. The absorption of oxygen and of albuminous liquids, and the exhalation of carbonic acid, so far as it is produced, can readily take place through the simple membranes of

the egg; especially as the time occupied in the formation of the primary organs is very short, and the greater part of the process of development remains to be accomplished after the young animal leaves the egg.

But in birds and quadrupeds, the time required for the development of the embryo within the egg is longer. The young animal acquires a more perfect organization during the time that it remains inclosed by its membranes; and the processes of absorption and exhalation necessary for its growth, being increased in activity to a corresponding degree, require a special organ for their accomplishment. This organ, destined to bring the blood of the fœtus into relation with the atmosphere and external sources of nutrition, is the *allantois.*

In the frog, the internal blastodermic layer, forming the intestinal mucous membrane, is everywhere inclosed by the external layer, forming the integument. But in the higher animals a portion of this internal layer, which is the seat of the greatest vascularity, and which is destined to produce the allantois, is brought into contact with the external membrane of the egg for purposes of exhalation and absorption; and this can only be accomplished by opening a passage for it through the external blastodermic layer. This is done in the following manner by the formation of the *amnion.*

Soon after the body of the embryo has begun to be formed, by the thickening and involution of the external blastodermic layer, a secondary fold of this layer rises up on all sides about the edges of the newly-formed embryo; so that its body appears as if sunk in a kind of depression, and surrounded with a membranous ridge, as in Fig. 255. The embryo (*c*) is here seen in profile, with the external membranous folds, above mentioned, rising up in advance of the head, and behind the posterior extremity. The same thing takes place on the two sides of the fœtus, by the formation of lateral folds simultaneously with the appearance of those in front and behind. As these folds are destined to form the amnion, they are called the "amniotic folds."

Fig. 255.

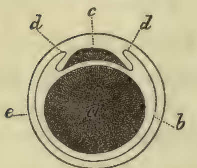


Diagram of the FECUNDATED EGG; showing the formation of the amnion.—*a.* Vitellus. *b.* External blastodermic layer. *c.* Body of the embryo. *d, d.* Amniotic folds. *e.* Vitelline membrane.

The amniotic folds continue to grow, extending forward, backward, and laterally, until they approach each other at a point over the back of the embryo (Fig. 256). Their opposite edges afterward come in contact with each other at this point, and adhere together, so as to shut in a space (Fig. 256, *b*) between their inner surface and the body of the embryo. This space, which contains a thin layer of clear fluid, is the amniotic cavity.

There now appears a prolongation or diverticulum (Fig. 256, *c*), growing from the posterior portion of the intestinal canal, and following the course of the amniotic fold which has preceded it; occupying, as it gradually enlarges and protrudes, the space left vacant by the

rising up of the amniotic fold. This diverticulum is the commencement of the allantois. It is an elongated membranous sac, continuous with the posterior portion of the intestine, and containing bloodvessels derived from those of the intestinal circulation. The cavity of the allantois is also continuous with the cavity of the intestine.

Fig. 256.

Diagram of the FECUNDATED EGG, farther advanced —*a*. Umbilical vesicle. *b*. Amniotic cavity. *c*. Allantois.

After the amniotic folds have approached and touched each other, as above described, over the back of the embryo, the adjacent surfaces, thus brought in contact, fuse together, so that the cavities of the two folds, coming respectively from front and rear, are separated only by a single membranous partition (Fig. 257, *c*) running from the inner to the outer lamina of the amniotic folds. This partition is soon afterward atrophied and disappears; and the inner and outer laminæ become consequently separated from each other. The inner lamina (Fig. 257, *a*) which remains continuous with the integument of the fœtus, inclosing the body of the embryo in a distinct cavity, is called the *amnion* (Fig. 258, *b*), and its cavity is known as the amniotic cavity. The outer lamina of the amniotic fold, on the other hand (Fig. 257, *b*), recedes farther and farther outward, until it comes in contact with the original vitelline membrane, still covering the exterior of the egg. It at last fuses with the vitelline membrane and unites with its substance, so that the two form but one. This membrane, resulting from the union and consolidation of two others, constitutes then the external investing membrane of the egg.

Fig. 257.

Diagram of the FECUNDATED EGG, with allantois nearly complete.—*a*. Inner lamina of amniotic fold. *b*. Outer lamina of ditto. *c*. Point where the amniotic folds come in contact. The allantois is seen penetrating between the inner and outer laminæ of the amniotic folds.

The allantois, in the mean time, increases in size and vascularity. Following the course of the amniotic folds as before, it insinuates itself between them, and thus comes in contact with the external membrane above described. It then begins to expand laterally, enveloping more and more the body of the embryo, and bringing its vessels into contact with the external investing membrane of the egg.

By a continuation of this process, the allantois at last envelops completely the body of the embryo, together with the amnion; its two extremities coming in contact with each other, and fusing together over the back of the embryo, in the same manner as the amniotic folds had previously done. (Fig. 258.) It lines, therefore, the whole internal surface of the investing membrane with a flattened, vascular sac, the

vessels of which come from the interior of the body of the embryo, and which still communicates with the cavity of the intestinal canal.

It is evident, accordingly, that there is a close connection between the formation of the amnion and that of the allantois. For it is only by this means that the allantois, which is an extension of the internal blastodermic layer, can come to be situated outside the embryo and the amnion, and thus brought into relation with surrounding media. The two laminæ of the amniotic folds, by separating from each other as above described, open a passage for the allantois, and allow it to come in contact with the external membranous investment of the egg.

Fig. 258.

Diagram of the FECUNDATED EGG, with the allantois fully formed. — *a.* Umbilical vesicle. *b.* Amnion. *c.* Allantois.

Physiological Action of the Allantois.—The physiological action of the allantois, in its simplest form, may be studied with advantage in the fowl's egg, where it forms an extensive and highly vascular organ, but does not present any important modifications of its original structure.

The egg of the fowl contains, when first laid, an abundant deposit of semi-solid albuminous matter in which the yolk is enveloped. This affords, in connection with the yolk, a sufficient quantity of moisture and organic nutriment for the growth of the embryo. The necessary warmth is supplied by the body of the fowl in incubation; and the atmospheric gases can pass and repass without difficulty through the porous shell and its lining membranes. On the commencement of incubation, a liquefaction takes place in the albumen immediately above that part of the yolk which is occupied by the blastoderm; so that the vitellus rises toward the surface, by virtue of its specific gravity, and the blastoderm comes to be placed almost immediately underneath the lining membrane of the egg-shell. The body of the embryo is thus placed in the most favorable position for the reception of warmth and other necessary external influences. The liquefied albumen is absorbed by the vitelline membrane, and the yolk thus becomes larger, softer, and more diffluent than before the commencement of incubation.

As soon as the circulatory apparatus of the embryo has been fairly formed, two minute arteries are seen to run out from its lateral edges and spread into the neighboring parts of the blastoderm, breaking up into inosculating branches, and covering the adjacent portions of the yolk with a plexus of capillary bloodvessels. The space occupied in the blastoderm by these vessels is called the *area vasculosa.* The blood is returned from it to the body of the embryo by two veins which penetrate beneath its edges, one near the head and one near the tail.

The area vasculosa increases in extent as the development of the embryo proceeds, and its circulation becomes more active. It covers the upper half or hemisphere of the yolk; and then, passing this point,

it embraces more and more of the inferior hemisphere, its vessels converging toward the opposite pole of the yolk.

The function of the area vasculosa is to absorb nourishment from the cavity of the vitelline sac. As the albumen liquefies during the process of incubation, it passes by endosmosis into the vitelline cavity; the whole yolk growing constantly larger and more fluid in consistency. The blood of the embryo, circulating in the vessels of the area vasculosa, absorbs the oleagino-albuminous matters of the vitellus, and, carrying them back to the embryo by the returning veins, supplies the tissues and organs with appropriate nourishment.

During this period the amnion and the allantois have been also in process of formation. At first the body of the embryo lies upon its abdomen, as heretofore described; but, as it increases in size, it alters its position so as to lie upon its left side. The allantois, emerging from the posterior portion of the abdominal cavity, turns upward over the body of the embryo, and comes in contact with the shell membrane. It then spreads out rapidly, extending toward the two extremities and down the sides of the egg, enveloping the embryo and the vitelline sac, and taking the place of the albumen which has been liquefied and absorbed.

The umbilical vesicle is at the same time formed by the separation of part of the yolk from the abdomen of the chick; and the vessels of the original area vasculosa, which were at first distributed over the yolk, now ramify upon the surface of the umbilical vesicle.

At last the allantois, by its continued growth, envelops nearly the whole of the remaining contents of the egg; so that toward the later periods of incubation, at whatever point we open the egg, the internal surface of the shell membrane is found to be lined with a vascular expansion. This expansion is the allantois, supplied by arteries emerging from the body of the embryo.

The allantois is accordingly adapted, by its structure and position, to perform the office of a respiratory organ. The air penetrates from the exterior through the porous shell and its lining membranes, and acts upon the blood in the vessels of the allantois much in the same manner that the air in the lungs of the adult animal acts upon the blood in the pulmonary capillaries. Examination of the egg, at various periods of incubation, shows that changes take place in it which are entirely analogous to those of respiration.

The egg, in the first place, during the development of the embryo, loses water by exhalation. This exhalation is not a simple effect of evaporation, but is the result of the nutritive changes going on in the interior of the egg; since it does not take place, except in a comparatively slight degree, in unimpregated eggs, or in those which are not incubated, though freely exposed to the air. The exhalation of fluid is also essential to the processes of development; since it has been found, in hatching eggs by artificial warmth, that if the air of the hatching chamber become unduly charged with moisture, so as to retard or prevent further exhalation, the development of the embryo is arrested. The loss of weight during natural incubation, mainly due to the exhalation

of water, has been found by Baudrimont and St. Ange[1] to be over 15 per cent. of the entire weight of the egg.

Secondly, the egg absorbs oxygen and exhales carbonic acid. The two observers above mentioned, ascertained that during eighteen days' incubation, the egg absorbs nearly 2 per cent. of its weight of oxygen, while the quantity of carbonic acid exhaled from the sixteenth to the nineteenth day amounts to nearly $\frac{1}{6}$ of a gramme in twenty-four hours. It is also observed that in the egg during incubation, as well as in the adult animal, more oxygen is absorbed than is returned by exhalation under the form of carbonic acid.

The allantois, however, is not simply an organ of respiration; it takes part also in the absorption of nutritious matter. As the process of development advances, the skeleton of the young chick, at first cartilaginous, begins to ossify. The calcareous matter, necessary for ossification, is in great part derived from the shell. The shell is perceptibly lighter and more fragile toward the end of incubation than at first; and, at the same time, the calcareous ingredients of the bones increase in quantity. The lime-salts, requisite for ossification, are apparently absorbed from the shell by the vessels of the allantois, and thus transferred to the skeleton of the growing chick; so that, in the same proportion that the former becomes weaker, the latter grows stronger. The diminution in density of the shell is connected not only with the development of the skeleton, but also with the final escape of the chick from the egg. This deliverance is accomplished mainly by the movements of the chick itself, which become, at a certain period, sufficiently vigorous to break out an opening in the attenuated shell. The first fracture is generally accomplished by a stroke from the end of the bill; and it is precisely at this point that the solidification of the skeleton is most advanced. The egg-shell, therefore, which at first serves for the protection of the embryo, afterward furnishes the materials which are used to accomplish its own demolition, and at the same time to effect the escape of the fully developed chick.

Toward the latter periods of incubation, the allantois becomes more adherent to the internal surface of the shell-membrane. At last, when the chick, arrived at the full period of development, escapes from its confinement, the allantoic vessels are torn off at the umbilicus; and the allantois itself, cast off as an effete organ, is left behind in the cavity of the abandoned shell.

Both the amnion and the allantois are, therefore, formations belonging to the embryo, and constituting, for a time, accessory but essential parts of its organization. Developed from the peripheral portions of the outer and inner blastodermic layers, they are important organs during the middle and latter periods of incubation; but when the chick has become fully developed, and is ready to carry on an independent existence, they are thrown off as obsolete structures, their place being afterward supplied by organs belonging to the adult condition.

[1] Développement du Fœtus. Paris, 1850, p. 143.

CHAPTER X.

DEVELOPMENT OF THE IMPREGNATED EGG AND ITS MEMBRANES IN THE HUMAN SPECIES. AMNION AND CHORION.

In the human species, as well as in the lower animals, the fœtus is enveloped in two membranes, an inner and an outer, derived respectively from extensions of the external and internal blastodermic layers, and consequently parts of the embryonic organism. While the inner of these envelopes has the same characters as elsewhere, the outer one presents such modifications of structure as to have received a distinct name. In the lower animals, therefore, the fœtal membranes are called the amnion and the allantois; in man, they are known as the amnion and the chorion.

Amnion.

The formation of the amnion in the human species takes place in the same manner as that already described (p. 740), namely, by the growth of a circumvallation or fold of the external blastodermic layer, which extends itself in such a way that its edges meet and coalesce over the back of the embryo, thus inclosing it in a distinct cavity.

Fig. 259.

Human Embryo and its Envelopes, about the end of the first month.—1. Umbilical vesicle. 2. Amnion. 3. Chorion.

Fig. 260.

Human Embryo and its Envelopes, at the end of third month; showing the enlargement of the amnion.

At the time of its formation, the amnion closely embraces the body of the embryo, so that there is hardly any space between the two; the opposite surfaces lying in contact with each other, like those of the

peritoneum in the adult. This space afterward enlarges somewhat and becomes the amniotic cavity, containing a little colorless, transparent, serous fluid, the amniotic fluid. But throughout the earlier periods of development the cavity of the amnion is small, as compared with that of the entire egg; and the space between the amnion and the external membrane, or chorion (Fig. 259), is occupied by an amorphous gelatinous material, in which the umbilical vesicle and its stem lie imbedded.

Subsequently the amnion enlarges more rapidly, in comparison with the remaining parts of the egg, and thus encroaches upon the layer of gelatinous material by which it is surrounded. At the same time the amniotic fluid increases in quantity (Fig. 260); so that a considerable space is left around the embryo, which is supported by the uniform pressure of the surrounding fluid. The amnion continues to enlarge at this increased rate of growth until about the beginning of the fifth month, when it comes in contact with the inner surface of the chorion; the gelatinous material previously intervening between them having disappeared, or being reduced to a nearly imperceptible layer.

Chorion.

The chorion, in the human species, is the external enveloping membrane of the embryo. It originates, like the corresponding envelope in the lower animals, by a protrusion or outgrowth from the posterior portion of the primitive alimentary canal, which, insinuating itself between the two laminæ of the amniotic fold, spreads gradually over and around the inner lamina or amnion proper, so as to occupy finally a position outside of it. It there meets with the two thin layers which have preceded it in this situation, namely the outer lamina of the amniotic fold, and the original vitelline membrane of the egg. But these two layers, ceasing to grow, while the new structures and the whole egg are rapidly enlarging, disappear as distinct membranes, and their place is taken by the chorion, which thus becomes, alone, the external investment of the egg.

So far, the history of development of the chorion is the same with that of the allantois. But the peculiarity which distinguishes it is that, in expanding over and around the other parts, it does not present the form of a double sac containing fluid, but of a single vascular sheet or membrane, like that of the skin. It is on this account that in the human species it is called the *chorion*, while in the lower animals it retains the name of allantois.

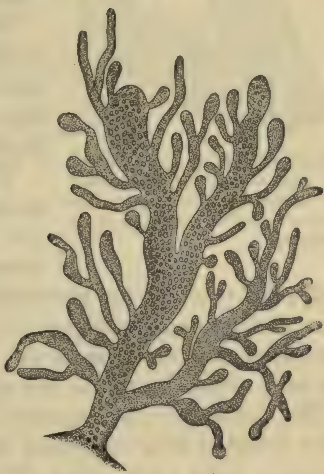
Nevertheless, the chorion, like the allantois, is at its commencement a hollow sac or canal with a blind extremity, the cavity of which is a continuation of that of the intestine. But this cavity does not extend at any time for more than a short distance outside the body of the embryo. Beyond this point it becomes obliterated, its membranous walls remaining in contact with and adherent to each other, forming a solid membrane, as above described. Inside the body of the embryo, on the other hand, it retains the form of a membranous sac; and this

portion afterward becomes, in the process of further development, the urinary bladder. The rounded cord or "urachus," which, in the adult, runs from the superior fundus of the bladder to the situation of the umbilicus in the abdomen, is the vestige of the obliterated canal of the primitive chorion.

The next peculiarity of the chorion is, that *it becomes shaggy.* Even while the egg is still very small, and has but recently found its way into the uterine cavity, its exterior is already covered with transparent villi (Fig. 259), which increase the extent of its surface, and assist in the absorption of fluids from without. The villi are at this time quite simple in form, and homogeneous in structure.

As the egg increases in size, the villi elongate, and become ramified by the repeated budding of lateral offshoots. After this process has continued for some time, the outer surface of the chorion presents a uniformly shaggy appearance, owing to its being covered everywhere with compound villosities.

Fig. 261.



Compound villosity of the HUMAN CHORION, ramified extremity. From a three months' fœtus. Magnified 30 diameters.

The villosities, when examined by the microscope, have an exceedingly characteristic appearance. They originate from the surface of the chorion by a somewhat narrow stem, and divide into secondary and tertiary branches of varying size and figure; some of them filamentous, others club-shaped, many of them irregularly swollen at various points. All terminate by rounded extremities, giving to the whole tuft a certain resemblance to some varieties of sea-weed. The larger trunks and branches of the villosity are seen to contain minute nuclei, imbedded in a nearly homogeneous, or finely granular substratum. The smaller ones appear, under a low magnifying power, simply granular in texture.

The villi of the chorion are quite unlike any other structure to be met with in the body. Whenever we find, in the uterus, any portion of a membrane having villosities of this character, it is certain that pregnancy has existed; for such villosities can only belong to the chorion, and the chorion itself is a part of the fœtus. The presence of portions of a shaggy chorion is therefore as satisfactory proof of the existence of pregnancy, as if the body of the fœtus itself had been found.

While the villosities just described are in process of formation, the chorion receives a supply of bloodvessels from the interior of the body of the embryo. The arteries, which are a continuation of those dis-

tributed to the alimentary canal, pass out along the canal of communication to the chorion and ramify over its surface. The embryo at this time has reached such an activity of growth that it requires to be supplied with nourishment by means of vascular absorption, instead of the slow process of imbibition hitherto taking place through the comparatively structureless villi of the chorion. The capillary bloodvessels, with which the chorion is supplied, begin to penetrate the substance of its villosities. They enter the base or stem of each villus, and, following the division of its compound ramifications, reach the rounded extremities of its terminal offshoots. Here they turn upon themselves in loops (Fig. 262), and retrace heir course, to unite finally with the venous runks of the chorion.

Fig. 262.

Extremity of a VILLOSITY OF THE CHORION, magnified 180 diameters; showing the arrangement of bloodvessels in its interior.

The villi of the chorion are, accordingly, analogous in structure and function to those of the intestine; their power of absorption corresponding with the abundance of their ramifications, and the extent of their vascularity.

The bloodvessels of the chorion, furthermore, are all derived from the abdomen of the fœtus; and all substances absorbed by them are transported to the interior of the body, and used for the nourishment of its tissues. The chorion, therefore, as soon as its villi and bloodvessels are completely developed, becomes an active organ in the nutrition of the fœtus; and constitutes the only means by which new material is introduced from without.

The third event of importance in the history of the chorion is that after being at first uniformly shaggy throughout, it afterward *becomes partially bald.* (Fig. 260.) This change begins about the end of the second month, commencing at a point opposite the insertion of the fœtal bloodvessels. The villosities of this region cease growing; and while the entire egg continues to enlarge, they fail to keep pace with the progressive expansion of the chorion. They accordingly become at this part thinner and more scattered, leaving the surface of the chorion comparatively bald. This baldness increases in extent, spreading over the adjacent portions of the chorion, until at least two-thirds of its surface have become nearly or quite destitute of villosities.

At the opposite pole of the egg, namely, that which corresponds with the insertion of the fœtal bloodvessels, the villosities of the chorion, instead of becoming atrophied, continue to grow; and this portion becomes even more shaggy and thickly set than before. The consequence is that the chorion afterward presents a different appearance at different parts of its surface. The greater part is smooth; but a certain portion, constituting about one-third of the whole, is covered with a soft, spongy mass of long, thickly-set, compound villosities. It is this thickened

portion which is afterward concerned in the formation of the *placenta;* while the remaining smooth portion continues to be known under the name of the chorion. The placental portion of the chorion becomes distinctly limited in outline by about the end of the third month.

The vascularity of the chorion keeps pace, in its different parts, with the atrophy and development of its villosities. As the villosities shrivel and disappear over a part of its extent, the bloodvessels with which they were supplied diminish in abundance; and the smooth portion of the chorion finally shows only a few straggling vessels running over its surface, but not connected with any abundant capillary plexus. In the thickened portion, on the other hand, the bloodvessels lengthen and ramify to an extent corresponding with that of the villosities in which they are situated. The arteries, coming from the abdomen of the fœtus, divide into branches which enter the villi, and penetrate through their whole extent; forming, at the placental portion of the chorion, a mass of tufted and ramified vascular loops, while the rest of the membrane has a comparatively scanty vascular supply.

The chorion, accordingly, is the external investing membrane of the egg, produced by an outgrowth from the body of the embryo; and the placenta, so far as it consists of the fœtal membranes, is a part of the chorion, distinguished from the rest by the local development of its villi and bloodvessels.

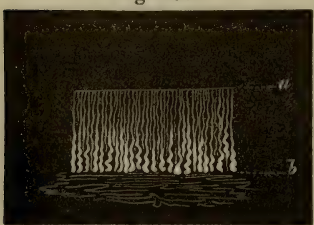
CHAPTER XI.

DEVELOPMENT OF THE DECIDUAL MEMBRANE, AND ATTACHMENT OF THE EGG TO THE UTERUS.

In the human species, where the development of the embryo is completed within the cavity of the uterus, the egg depends for its nutrition and growth upon materials derived from the organism of the female parent. The immediate source of supply for this purpose is the mucous membrane of the uterus, which becomes unusually developed and increased in functional activity during the period of gestation. The uterine mucous membrane, when thus modified in structure, is known as the decidual membrane, or the *decidua.* It has received this name because it is exfoliated and discharged at the same time that the egg itself is expelled from the uterus.

The mucous membrane of the body of the uterus, in the unimpregnated condition, is thin and delicate, and presents a smooth internal surface. There is no distinct layer of connective tissue between it and the muscular substance of the uterus; so that the mucous membrane cannot here, as in most other organs, be readily separated by dissection from the subjacent parts. The structure of the mucous membrane, however, is sufficiently well marked. It consists, throughout, of tubular follicles, ranged side by side, and running perpendicularly to its free surface. Near this surface, they are nearly straight; but toward the deeper part of the mucous membrane, where they terminate in blind extremities, they become more or less wavy or spiral in their

Fig. 263.



UTERINE MUCOUS MEMBRANE, from the unimpregnated uterus, in vertical section. *a.* Free surface. *b.* Attached surface. Magnified about 10 diameters.

Fig. 264.

UTERINE TUBULES, from the mucous membrane of an unimpregnated human uterus. Magnified 125 diameters.

course. The tubules are about 0.05 millimetre in diameter, and are lined with columnar epithelium. They occupy the entire thickness of the uterine mucous membrane, their closed extremities resting upon the subjacent muscular tissue, while their mouths open into the cavity of the uterus. A few fine bloodvessels penetrate the mucous membrane from below, and, running upward between the tubules, encircle their superficial extremities with a capillary network. There is no connective tissue in the uterine mucous membrane, but only a few isolated nuclei and spindle-shaped fibre-cells, scattered between the tubules.

Decidua Vera.—As the fecundated egg descends through the Fallopian tube, the uterine mucous membrane takes on an increased activity of growth. It becomes tumefied and vascular; and, as it increases in thickness, it projects, in rounded eminences or folds, into the uterine cavity. (Fig. 265.) In this process the uterine tubules increase in length, and also become wider; so that their open mouths may be readily seen by the naked eye upon the uterine surface, as numerous minute perforations. According to the observations of Kölliker, so early as the end of the first week they have increased to three or four times their original length and width, so that they measure at this time on the average nearly 0.20 millimetre in diameter. The bloodvessels of the mucous membrane also enlarge and communicate freely with each other; the vascular network between and around the tubules becoming more extensive and abundant. The internal surface of the uterus, after this process has been for some time going on, presents a thick, rich, soft, velvety, and vascular lining, quite different in appearance from that which is to be found in the unimpregnated condition. It is now known as the decidua; and in order to distinguish it from a similar growth of subsequent formation, it has received the special name of the *decidua vera.*

The production of the decidua is confined to the body of the uterus, the mucous membrane of the cervix taking no part in the process, but retaining its original appearance. The decidual membrane commences above, at the orifices of the Fallopian tubes, and ceases below, at the situation of the os internum. The cavity of the cervix, meanwhile, is filled with an abundant secretion of its peculiarly viscid mucus, which blocks up its passage, and protects the internal cavity. If the uterus be opened, therefore, in this condition, its internal surface will be seen lined with the decidua vera, which is continuous, at the os internum, with the unaltered mucous membrane of the cervix uteri.

Decidua Reflexa.—As the fecundated egg passes the lower orifice of the Fallopian tube, it insinuates itself between the opposite surfaces of the uterine mucous membrane, and becomes lodged in one of the furrows or depressions between the folds of the decidua. (Fig. 265.) At this situation an adhesion subsequently takes place between the external membranes of the egg and the uterine decidua. At the point where the egg thus becomes fixed, a still more rapid development takes place in the uterine mucous membrane. Its projecting folds grow up around

the egg in such a manner as to partially inclose it in a kind of circumvallation, and to shut it off, more or less completely, from the general

Fig. 265.

IMPREGNATED UTERUS; showing formation of decidua. The decidua is represented in black; and the egg is seen, at the fundus of the uterus, engaged between two of its projecting folds.

Fig. 266.

IMPREGNATED UTERUS, with projecting folds of decidua growing up around the egg. The narrow opening, where the edges of the folds approach each other, is seen over the most prominent portion of the egg.

cavity of the uterus. (Fig. 266.) The egg thus comes to be contained in a special cavity of its own, which still communicates for a time with the general cavity of the uterus, by an opening situated over its most prominent portion. As the process of growth goes on, this opening becomes narrower, while the decidual folds approach each other over the surface of the egg. At last these folds touch each other and unite, forming a kind of cicatrix which remains for a certain time, to mark the situation of the original opening.

Fig. 267.

IMPREGNATED UTERUS; showing the egg completely inclosed by the decidua reflexa.

When the development of the uterus has reached this point (Fig. 267), the egg is completely inclosed in a cavity of its own; being everywhere covered with a decidual layer of new formation, which has gradually enveloped it, and by which it is concealed from view when the uterine cavity is laid open. This newly-formed layer, enveloping the projecting portion of the egg, is called the *Decidua reflexa;* because it is reflected over the egg from the general surface of the uterine mucous membrane. The orifices of the uterine tubules, in consequence of the manner in which the decidua reflexa is formed, are to be seen not only on its external surface, or that which looks toward the cavity of the uterus, but also on its internal surface, or that which looks toward the egg.

The decidua vera, therefore, is the original mucous membrane lining the surface of the uterus. The decidua reflexa is a new formation, which grows up around the egg and incloses it in a distinct cavity.

If abortion occur at this time, the mucous membrane of the uterus, that is, the decidua vera, is thrown off, and brings with it the egg and the decidua reflexa. On examining the mass so discharged, the egg will be found imbedded in the substance of the decidual membrane. One side of the membrane, where it has been torn away from its attachment to the uterus, is ragged ; the other side, corresponding to the cavity of the uterus, is smooth or gently convoluted, and exhibits distinctly the orifices of the uterine tubules ; while the egg itself can only be extracted by cutting through the decidual membrane, either from one side or the other, and opening in this way the special cavity in which it is inclosed.

During the formation of the decidua reflexa, the entire egg, as well as the body of the uterus which contains it, has considerably enlarged. That portion of the uterine mucous membrane situated immediately underneath the egg, and to which it first became attached, has also continued to increase in thickness and vascularity. The remainder of the decidua vera, however, ceases to grow as before, and no longer keeps pace with the increasing size of the egg and of the uterus. It is still thick and vascular at the end of the third month ; but after that period it becomes comparatively thinner and less glandular, while the activity of growth is concentrated in the egg, and in that portion of the uterine mucous membrane with which it is in immediate contact.

Attachment of the Egg to the Uterus.—While the above changes are taking place in the lining membrane of the uterus, the formation of the embryo, and the development of the amnion and chorion have been going on simultaneously ; and soon after the entrance of the egg into the uterine cavity, the chorion is everywhere covered with projecting villosities. These villosities insinuate themselves into the uterine tubules, or between the folds of the decidual surface ; penetrating in this way into little cavities of the uterine mucous membrane. When the formation of the decidua reflexa is completed, the chorion has already become uniformly shaggy ; and its villosities, spreading in all directions from its external surface, penetrate everywhere both into the decidua vera beneath it and into the decidua reflexa with which it is covered. In this way the egg becomes entangled with the decidua, and cannot be readily separated from it without rupturing some of the filaments which have grown from its surface, and have penetrated the substance of the decidua. The nutritious fluids, exuded from the glandular textures of the decidua, are now imbibed by the villosities of the chorion ; and a more rapid supply of nourishment

Fig. 268.

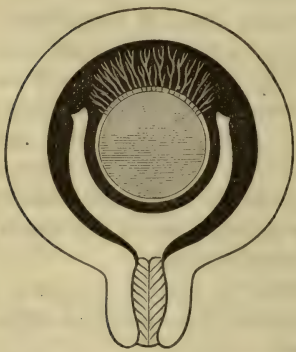
IMPREGNATED UTERUS, showing the connection between the villosities of the chorion and the decidual membranes.

is thus provided, corresponding in abundance with the greater size of the egg.

Very soon the activity of absorption is still further increased. The chorion becomes vascular, by the formation of bloodvessels emerging from the body of the embryo and penetrating everywhere into the villosities with which it is covered. Each villosity then contains a vascular loop, imbedded with itself in the substance of the decidua, and serving to absorb from the uterine mucous membrane the materials for the growth of the embryo.

Subsequently, the vascular tufts of the chorion, which are at first uniformly distributed over its surface, disappear throughout the greater part of its extent, while they become still further developed and concentrated at a particular point, the situation of the future placenta. This is the spot at which the egg is in contact with the decidua. Here, both the decidual membrane and the tufts of the chorion continue to increase in thickness and vascularity; while elsewhere, over the prominent portion of the egg, the chorion not only becomes bare of villosities and comparatively destitute of bloodvessels, but the decidua reflexa, which is in contact with it, also loses its activity of growth and becomes expanded into a thin layer, without any remaining trace of glandular follicles.

Fig. 269.



PREGNANT UTERUS; showing the formation of the placenta by the united development of a portion of the decidua and the villosities of the chorion.

The uterine mucous membrane is therefore developed, during gestation, in such a way as to provide for the nourishment of the embryo in the different stages of its growth. At first, the whole of it is uniformly increased in thickness (decidua vera). Next, a portion of it grows upward around the egg, and covers its projecting surface (decidua reflexa). Afterward, both the decidua reflexa and the greater part of the decidua vera diminish in the activity of their growth, and lose their importance as a means of nourishment for the embryo; while that part which is in contact with the vascular tufts of the chorion continues to grow, becoming excessively developed, and taking part in the formation of the placenta.

CHAPTER XII.

THE PLACENTA.

In all instances in which, as in man and the mammalians, the embryo is dependent, for the materials of its growth, upon nutritious fluids supplied by the uterus, the communication between them is established by means of two vascular membranes. One of these membranes, the chorion or the allantois, is a part of the embryo; the other is the mucous membrane of the uterus. By their more or less intimate juxtaposition, the fluids transuded from the bloodvessels of the mother are absorbed by those of the embryo, and thus a transfer of nutriment takes place from the maternal to the fœtal organism.

In some species of animals, the connection between the maternal and fœtal membranes is a simple one. In the pig, for example, the uterine mucous membrane is everywhere uniformly vascular; its only peculiarity consisting in the presence of transverse folds, which project inward from its surface, like the valvulæ conniventes of the small intestine. The external investing membrane of the egg, or the allantois, is also smooth and uniformly vascular. No special development of tissue or of vessels occurs at any part of these membranes, and no adhesion takes place between them. The vascular allantois of the fœtus is simply in close apposition with the vascular mucous membrane of the uterus; each of the two contiguous surfaces following the undulations

Fig. 270.

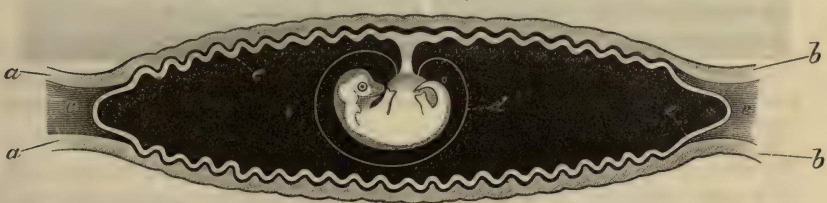


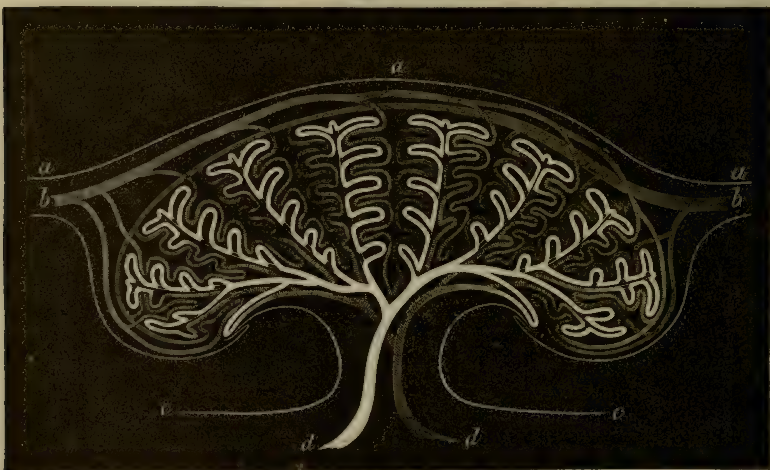
Diagram of the **Fœtal Pig**, with its membranes, in the uterus; showing the relation of the allantoic and uterine surfaces.—*a*, *a*, *b*, *b*. Walls of the uterus. *c*, *c*. Cavity of the uterus. *d*. Amnion. *e*, *e*. Allantois.

presented by the other. (Fig. 270.) By this arrangement, transudation and absorption take place from the bloodvessels of the mother to those of the fœtus, in sufficient quantity to provide for the nutrition of the latter. When parturition takes place, a moderate contraction of the uterus is sufficient to expel its contents. The egg, displaced from its original position, slides forward over the surface of the uterine mucous

membrane, and is discharged without any hemorrhage or laceration of the parts.

In other instances, there is a more intimate connection, at certain points, between the fœtal and maternal structures. In the cow, the sheep, and the ruminating animals generally, the external membrane of the egg, beside being everywhere supplied with branching bloodvessels, presents, scattered over its surface, a large number of distinct rounded or oval spots, at each of which it is covered with thickly set, tufted, vascular prominences. These spots are called *cotyledons*, or cups, because each one is surrounded by a raised rim or fold, which embraces a corresponding rounded mass projecting from the internal surface of the uterus. This projecting portion of the uterine mucous membrane is also abundantly supplied with bloodvessels; and the tufted vascular loops projecting from the surface of the fœtal membrane (Fig. 271, *b*, *b*) dip down into its substance and are entangled with those belonging to

Fig. 271.



COTYLEDON, from the pregnant uterus of the cow.—*a*. Internal surface of the allantois. *b*, *b*. Fœtal bloodvessels. *c*, *c*. Surface of uterine mucous membrane. *d*, *d*. Maternal bloodvessels.

the uterus (*d*, *d*). There is no absolute adhesion between the two sets of vessels, but only an interlacement of their ramified extremities; and by careful manipulation the fœtal portion, with its villosities, may be extricated from the maternal portion without the laceration of either.

In the carnivorous animals, a similar highly developed, vascular portion of the allantois runs, in the form of a single broad belt or band, round its middle part; and this corresponds in situation with an equally developed zone of the uterine mucous membrane. Here the fœtal and maternal structures are adherent to each other; while, elsewhere, toward the two extremities of the egg, they lie simply in contact. When gestation comes to an end in these animals, and the fœtus, with

its membranes, is expelled, the thickened zone of uterine mucous membrane is detached at the same time, and its place is afterward made good by a new growth.

In the human species, as shown in the preceding chapter, the permanently thickened portions of the chorion and decidua, united with each other by mutual interpenetration and growth, form a single, flattened, cake-like mass of rounded form, occupying rather less than one-third of the surface of the chorion, and corresponding to a similar extent of the inner surface of the uterus. This mass, consisting of the fœtal and maternal elements combined, is the *placenta.*

The complete development of the placenta takes place in the following manner:

The villi of the chorion, when first formed, penetrate into follicles situated in the substance of the uterine mucous membrane; and after becoming vascular, they are developed into tufted ramifications of bloodvessels, each one of which turns upon itself in a loop at the extremity. At the same time the uterine follicle, into which the villus has penetrated, enlarges to a similar extent; sending out branching diverticula, corresponding with the multiplied ramifications of the villus. The growth of the follicle and that of the villus thus go on simultaneously and keep pace with each other; the latter constantly advancing as the cavity of the former enlarges.

But it is not only the uterine follicles which increase in size and in complication of structure at this period. The capillary bloodvessels, which lie between them and ramify over their exterior, also become unusually developed. They enlarge and inosculate freely with each other; so that every uterine follicle is covered with a network of dilated capillaries, derived from the bloodvessels of the original decidua.

Fig. 272.

Extremity of a FŒTAL TUFT, from the human placenta at term, in its recent condition.—*a, a.* Capillary bloodvessels. Magnified 135 diameters.

As the formation of the placenta goes on, the anatomical arrangement of the fœtal bloodvessels remains the same. They continue to form vascular loops, penetrating deeply into the decidual membrane; only they become more elongated, and their ramifications more abundant and tortuous. The maternal capillaries, however, on the outside of the uterine follicles, become considerably altered in their anatomical relations. They enlarge in all directions, and, by encroaching upon the spaces situated between them, fuse successively with each other; and, losing gradually in this

way the characters of a capillary network, become dilated into sinuses, which communicate freely with the vessels in the muscular walls of the uterus. As the original capillary plexus occupied the entire thickness of the hypertrophied decidua, the vascular sinuses, into which it is thus converted, are equally extensive. They commence at the external surface of the placenta, where it is in contact with the muscular walls of the uterus, and extend through its whole thickness, quite to the surface of the fœtal chorion.

As the maternal sinuses grow inward, the vascular tufts of the chorion grow outward, and extend also through the entire thickness of the placenta. In the latter periods of pregnancy, the development of the bloodvessels, both in the fœtal and maternal portions of the placenta, is so excessive that all the other tissues, which originally coexisted with them, have nearly disappeared. If a villus from the fœtal portion of the placenta be examined at this time by transparency, in the fresh condition (Fig. 272) it will be seen that its bloodvessels are covered only with a layer of homogeneous, or finely granular material, about 7 mmm. in thickness, in which are imbedded small oval-shaped nuclei, similar to those seen at an earlier period in the villosities of the chorion. The placental villus is now, therefore, hardly anything more than a congeries of ramified and tortuous vascular loops; its remaining substance having been atrophied and absorbed in the excessive growth of the bloodvessels, the abundance and development of which can be readily shown by injection from the umbilical arteries. (Fig. 273.) The uterine follicles have at the same time lost their original structure, and have become mere vascular sinuses, into which the tufted fœtal bloodvessels are received, as the villosities of the chorion were at first received into the uterine follicles.

Fig. 273.

Extremity of a FŒTAL TUFT of the human placenta; from an injected specimen. Magnified 40 diameters.

Finally, the walls of the fœtal bloodvessels having come into close apposition with the walls of the maternal sinuses, the two become adherent and fuse together; so that a time at last arrives when we can no longer separate the fœtal vessels, in the substance of the placenta, from the maternal sinuses, without lacerating either the one or the other, owing to the adhesion which has taken place between them.

The placenta, therefore, when perfectly formed, has the structure which is shown in the accompanying diagram (Fig. 274), representing a vertical section of the organ through its entire thickness. At *a*, *a*, is seen the chorion, receiving the umbilical vessels from the body of the fœtus through the umbilical cord, and sending out its compound and ramified vascular tufts into the substance of the placenta. At *b*, *b*, is the attached surface of the decidua, or uterine mucous membrane; and

at c, c, c, c, are the orifices of uterine vessels which penetrate it from below. These vessels enter the placenta in an extremely oblique direction, though they are represented in the diagram, for the sake of distinctness, as nearly perpendicular. When they have once penetrated

Fig. 274.

Vertical section of the PLACENTA, showing the arrangement of the maternal and fœtal bloodvessels.—*a*. *a*. Chorion. *b*, *b*. Decidua. *c*, *c*, *c*, *c*. Orifices of uterine sinuses.

the lower portion of the decidua, they immediately dilate into the placental sinuses (represented, in the diagram, in black), which extend through the whole thickness of the organ, closely embracing all the ramifications of the fœtal tufts. It will be seen, therefore, that the placenta, arrived at this stage of completion, is composed essentially of nothing but bloodvessels. The other tissues which originally entered into its structure have disappeared, leaving the bloodvessels of the fœtus entangled with and adherent to the bloodvessels of the mother.

There is, however, no direct communication between the fœtal and maternal vessels. The blood of the fœtus is always separated from the blood of the mother by a membrane which has resulted from the successive union and fusion of four different membranes, namely: first, the membrane of the fœtal villus; secondly, that of the uterine follicle; thirdly, the wall of the fœtal bloodvessel; and fourthly, the wall of the uterine sinus. The membrane, however, thus produced, is of great extent, owing to the abundant branching and subdivision of the fœtal tufts. These tufts, in which the blood of the fœtus circulates, are bathed everywhere, in the placental sinuses, with the blood of the mother; and the processes of absorption and exhalation go on between the two with a corresponding activity.

It is easy to demonstrate the arrangement of the fœtal tufts in the human placenta. They can be readily seen by the naked eye, and may

be traced from their attachment at the under surface of the chorion to their termination near the uterine surface of the placenta. The anatomical disposition of the placental sinuses is more difficult of examination. During life, and while the placenta is still attached to the uterus, they are filled, of course, with the blood of the mother, and occupy fully one-half the mass of the placenta. But when the placenta is detached, the maternal vessels belonging to it are torn off at their necks (Fig. 274, *c*, *c*, *c*, *c*), and the sinuses, being then emptied of blood by the compression to which the placenta is subjected, are apparently obliterated; and the fœtal tufts, falling together and lying in contact with each other, appear to constitute the whole of the placental mass. The existence of the placental sinuses, however, and their true extent, may be demonstrated in the following manner.

If we take the uterus of a woman who has died undelivered at the full term or thereabout, and open it in such a way as to avoid wounding the placenta, this organ will be seen remaining attached to the uterine surface, with all its vascular connections complete. Let the fœtus be now removed by dividing the umbilical cord, and the uterus, with the placenta attached, placed under water, with its internal surface uppermost. If the end of a blowpipe be then introduced into one of the divided vessels of the uterine walls, and air forced in by gentle insufflation, we can easily inflate, first, the vascular sinuses of the uterus, and next, the deeper portions of the placenta; and lastly, the bubbles of air insinuate themselves everywhere between the fœtal tufts, and appear in the most superficial portions of the placenta, immediately underneath the transparent chorion (*a*, *a*, Fig. 274); thus showing that the placental sinuses, which freely communicate with the uterine vessels, occupy the entire thickness of the placenta, and are equally extensive with the tufts of the chorion. We have verified this fact in the above manner, on six different occasions, and in the presence of Prof. C. R. Gilman, Prof. Geo. T. Elliot, Prof. Henry B. Sands, Prof. T. G. Thomas, Dr. T. C. Finnell, and various other medical gentlemen of New York. The same thing has been done by Prof. A. Flint, Jr.,[1] with a similar result.

If the placenta be detached and examined separately, it will be found to present upon its uterine surface a number of openings, which are extremely oblique in position, and bounded on one side by a very thin crescentic edge. These are the orifices of the uterine bloodvessels, passing into the placenta and torn off at their necks, as above described; and by carefully following them with the probe and scissors, they are found to lead at once into extensive empty cavities (the placental sinuses), situated between the fœtal tufts. These cavities are filled during life with the maternal blood; and there is every reason to believe that before delivery, while the circulation is going on, the placenta is at least twice as large as after it has been detached and expelled from the uterus.

[1] Flint, Physiology of Man. New York, 1874, vol. v. p. 382.

The placenta, accordingly, is a double organ, formed partly by the chorion and partly by the decidua; and consisting of maternal and fœtal bloodvessels, entangled and united with each other.

The part which this organ takes in the development of the fœtus is of primary importance. From the date of its formation, at about the beginning of the fourth month, it constitutes the only channel through which nourishment is conveyed from the mother to the fœtus. The nutritious materials, which circulate in the blood of the maternal sinuses, pass through the intervening membrane, and enter the blood of the fœtus. The healthy or injurious regimen, to which the mother is subjected, will accordingly exert an influence upon the child. Even medicinal substances, taken by the mother and absorbed into the circulation, may transude through the placental vessels, and thus exert a specific effect upon the fœtal organization.

The placenta is, furthermore, an organ of exhalation as well as of absorption. The excrementitious matters, produced in the circulation of the fœtus, are undoubtedly in great measure disposed of by transudation through the walls of the placental vessels, to be afterward discharged by the excretory organs of the mother. The system of the mother may therefore be affected in this manner by influences derived from the fœtus. It has been observed in the lower animals, that when the female has two successive litters of young by different males, the young of the second litter will sometimes bear marks resembling those of the first male. In these instances, the influence which produces the external mark is transmitted by the first male to the fœtus, from the fœtus to the mother, and from the mother to the fœtus of the second litter.

It is also through the placental circulation that those disturbing effects are produced upon the nutrition of the fœtus, which result from sudden shocks or injuries inflicted upon the mother. There is little room for doubt that various deformities and deficiencies of the fœtus, conformably to the popular belief, originate, in certain cases, from nervous impressions experienced by the mother. The mode in which these effects may be produced is readily understood from the anatomy and functions of the placenta. It is well known how easily nervous impressions will disturb the circulation in the brain, the face, or the lungs; and the uterine circulation is quite as readily influenced by similar causes, as shown in cases of amenorrhœa and menorrhagia. If a nervous shock may excite premature contraction in the muscular fibres of the pregnant uterus and produce abortion, it is undoubtedly capable of disturbing the circulation of the blood in the same organ. But the fœtal circulation is dependent, to a great extent, on the maternal. The two sets of vessels are united in the placenta, and as the fœtal blood has much the same relation to the maternal, that the blood in the pulmonary capillaries has to the air in the pulmonary air-cells, it must be liable to derangement from similar causes. And lastly, as the nutrition of the fœtus is provided for wholly by the placenta, it will suffer from any disturbance of

the placental circulation. These effects may be manifested either in the general atrophy and death of the fœtus, or in the imperfect development of particular parts; just as in the adult a morbid action may operate upon the entire system, or may show itself in some one organ, which is more particularly sensitive to its influence.

CHAPTER XIII.

DISCHARGE OF THE FŒTUS AND PLACENTA. REGENERATION OF THE UTERINE TISSUES.

During the growth of the embryo and its membranes, and the development of the uterine mucous membrane into the decidua and placenta, the muscular tissue of the uterus also increases in thickness, while the whole organ enlarges, to accommodate the greater volume of its contents. This increase of substance, which is mainly due to an unusual growth in the muscular walls of the organ, gives it a sufficient degree of contractile power for the expulsion of the fœtus at the time of delivery.

The enlargement of the amniotic cavity, and the increased quantity of the amniotic fluid, also provide the requisite space and freedom for the intra-uterine movements of the fœtus. These movements begin to be perceptible about the fifth month, at which time the development of the muscular system has become sufficient to allow it a certain amount of functional activity. During the latter months of pregnancy they become more frequent and vigorous, and may often be felt by the hand of the observer applied to the abdomen over the region of the uterus.

The attachment of the embryo to the investing membranes of the egg is at first by a very short and comparatively wide funnel-shaped connection, consisting of the commencement of the chorion, a part of the amnion, and an abundant deposit of gelatinous material between the two, containing the stem of the umbilical vesicle. Subsequently, as the amniotic cavity enlarges, the body of the embryo recedes farther from the inner surface of the chorion, by the elongation of its connecting part; and this part consequently begins to present the appearance of a cord (Fig. 275). It is still surrounded with a thick layer of gelatinous matter, by which it is separated from its amniotic investment. As it emerges from the abdomen of the embryo at a point where the abdominal walls will afterward close round it, to form the umbilicus, it is known by the

Fig. 275.

Human Embryo and its Membranes, in the early period of gestation; showing the commencement of formation of the umbilical cord.

name of the *umbilical cord.* It contains the bloodvessels passing out from the body of the embryo to the chorion and placenta.

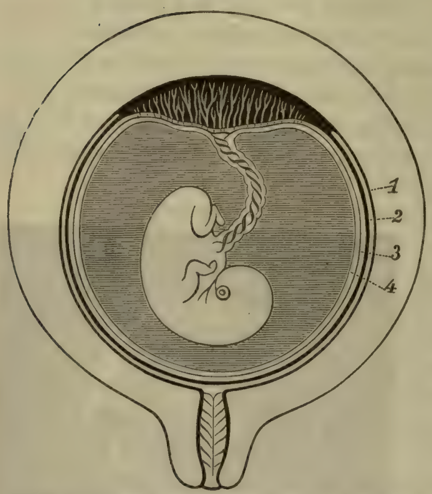
After the third month the umbilical cord and its bloodvessels elongate even more rapidly than is required by the increase in size of the amniotic cavity. They consequently assume a twisted form, the two umbilical arteries winding round the vein in a spiral direction.

The direction of the spiral is not always the same. Prof. McLane has recorded observations made in regard to this point upon 260 umbilical cords at term, partly in his private practice and partly at the Nursery and Child's Hospital, New York. Of this number, in 138 cases the direction of the spiral was from left to right; in 112 cases, from right to left; and in the 10 remaining instances it was doubtful, the twist being too imperfectly marked for decision. This gives nearly the following percentage as the result of all the observations:

Direction of the Spiral Twist of the Human Umbilical Cord.

From left to right	53 per cent.
From right to left	43 "
Indeterminate	4 "
	100

Fig. 276.



Pregnant Human Uterus and its Contents, about the end of the seventh month; showing the relations of the cord, placenta, and membranes.—1. Decidua vera. 2. Decidua reflexa. 3. Chorion. 4. Amnion.

There is, accordingly, no marked preponderance in frequency of the twist in either direction. Two cases of twins are included in the above list; in the first of which both umbilical cords turned from right to left; in the second, one of them turned from right to left, the other from left to right. In two instances, the cord presented turns in opposite directions in different parts of its length.

The gelatinous matter, already described as existing between the amnion and chorion, and which disappears elsewhere, accumulates, on the contrary, in the cord in considerable quantity, covering the vessels with a thick, elastic envelope, which protects them from accidental compression or obliteration. The whole is covered by an extension of the amnion, which is continuous at one extremity with the integument of the abdomen, and invests the cord with an uninterrupted sheath, like the finger of a glove.

The cord also contains, for a certain period, the pedicle or stem of the umbilical vesicle. The situation of this vesicle, necessarily, is always between the chorion and the amnion. Its pedicle gradually elongates with the growth of the umbilical cord; and the vesicle itself, which generally disappears soon after the third month, sometimes remains as late as the fifth, sixth, or seventh. According to Mayer, it may even be found, by careful search, at the termination of pregnancy. In the middle and latter periods of gestation, it presents itself as a small, flattened vesicle, situated beneath the amnion, at a variable distance from the insertion of the umbilical cord. A minute bloodvessel is often seen running to it from the cord, and ramifying upon its surface.

The decidua reflexa, during the latter months of pregnancy, is constantly distended by the increasing size of the egg, and finally pressed against the opposite surface of the decidua vera. By the end of the seventh month, the decidua vera and reflexa are in contact, though still distinct and capable of being easily separated. After that time, they become confounded with each other, forming at last only a single, thin, friable, semi-opaque layer, in which no trace of glandular structure can be discovered.

This is the condition of things at the termination of pregnancy. Then, the time having arrived for parturition to take place, the hypertrophied muscular walls of the uterus contract upon its contents, and the egg is discharged, together with the decidual membrane.

In the human species, as well as in most quadrupeds, the membranes of the egg are usually ruptured during the process of parturition; and the fœtus escapes first, the placenta and the rest of the appendages following a few moments afterward. Occasionally the egg is discharged entire, and the fœtus afterward liberated by the laceration of the membranes. In each case the mode of separation and expulsion is essentially the same.

The process of parturition, therefore, consists in a separation of the decidual membrane, which, on being discharged, brings away the ovum with it. The greater part of the decidua. vera, having fallen into a state of atrophy during the latter months of pregnancy, is by this time nearly destitute of vessels, and separates without perceptible hemorrhage. That portion which enters into the formation of the placenta is, on the contrary, excessively vascular; and when the placenta is separated, and its maternal vessels torn off at their insertion, a gush of blood takes place, which accompanies or immediately follows the birth of the fœtus. This hemorrhage, which occurs at the time of parturition, does not come immediately from the uterine vessels. It consists of blood which was contained in the placental sinuses, and which is expelled from them owing to the compression of the placenta by the muscular walls of the uterus. Since the whole amount of blood thus lost was previously employed in the placental circulation, and since the placenta itself is thrown off at the same time, no unpleasant effect is

produced upon the mother by such a hemorrhage, because the proportion of blood in the rest of the vascular system remains the same. Uterine hemorrhage at the time of delivery becomes injurious only when it continues after complete separation of the placenta; in which case it is supplied by the mouths of the uterine vessels, left open by failure of the uterine contractions. These vessels, in natural parturition, are instantly closed, after separation of the placenta, by the contraction of the uterine muscular fibres. They pass, as already mentioned, in an exceedingly oblique direction, from the uterus to the placenta; and the muscular fibres, which cross them transversely above and below, necessarily close their orifices by constriction as soon as they are thrown into a state of functional activity.

Regeneration of the Uterine Tissues after Delivery.—Both the mucous membrane and muscular tissue of the uterus, which are the seat of an unusual growth during pregnancy, are afterward replaced by corresponding tissues of new formation. The mucous membrane, or decidua, is discharged at the time of delivery; and the hypertrophied muscular tissue, which has served its purpose in the expulsion of the fœtus, undergoes soon afterward a process of retrogression and atrophy.

A remarkable phenomenon connected with the renovation of the uterine tissues, is the appearance in the uterus, during pregnancy, of a new mucous membrane, growing underneath the old, and ready to take the place of the latter after its discharge.

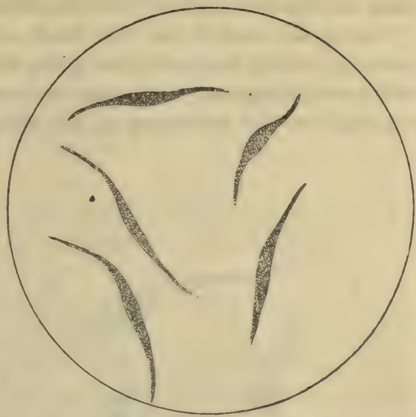
If the internal surface of the body of the uterus be examined immediately after parturition, it will be seen that at the spot where the placenta was attached, every trace of mucous membrane has disappeared. The muscular fibres of the uterus are here exposed and bare; while the mouths of the ruptured uterine sinuses are also visible, with their thin edges hanging into the cavity of the uterus, and their orifices plugged with bloody coagula.

Over the rest of the uterine surface the decidua vera has also disappeared. Here, however, notwithstanding the loss of the original mucous membrane, the muscular fibres are not perfectly bare, but are covered with a semi-transparent film, of whitish color and soft consistency. This film is an imperfect mucous membrane of new formation, which begins to be produced, underneath the old decidua vera, as early as the beginning of the eighth month. We have seen this very distinctly in the uterus of a woman who died undelivered at the above period. The old mucous membrane, or decidua vera, is at this time somewhat opaque, and of a slightly yellowish color, owing to partial fatty degeneration. It is easily separated from the subjacent parts, on account of the atrophy of its vascular connections; and the new mucous membrane, situated beneath it, is distinguishable by its fresh color and semi-transparent aspect.

The mucous membrane of the cervix uteri, which takes no part in the formation of the decidua, is not thrown off in parturition; and after

delivery it may be seen to terminate at the os internum by an uneven, lacerated edge, where it was formerly continuous with the decidua vera.

Fig. 277.



Muscular Fibres of the Unimpregnated Human Uterus; from a woman aged 40, dead of phthisis pulmonalis.

Subsequently, a regeneration of the mucous membrane takes place over the whole extent of the body of the uterus. The mucous membrane of new formation, which is already in existence at the time of delivery, becomes thickened and vascular; and glandular tubules are gradually developed in its substance. At the end of two months after delivery, according to Longet[1] and Heschl,[2] it has regained the natural structure of uterine mucous membrane. It unites at the os interum, by a linear cicatrix, with the mucous membrane of the cervix, and the traces of laceration at this spot afterward cease to be visible. At the point, however, where the placenta was attached, the regeneration of the mucous membrane is less rapid; and a cicatrix-like spot is often visible at this situation for several months after delivery.

Fig. 278.

Muscular Fibres of the Human Uterus, ten days after parturition; from a woman dead of puerperal fever.

The corresponding change in the muscular tissue of the uterus consists in the fatty degeneration of its fibres. The muscular fibres of the unimpregnated uterus are pale, flattened, spindle-shaped bodies (Fig. 277), homogeneous or faintly granular in appearance, and measuring about 50 mmm. in length. During gestation these fibres increase considerably in size. Their texture becomes more distinctly granular, and their outlines more strongly marked. An oval nucleus also shows itself in the central part of each fibre. The entire

[1] Traité de Physiologie. Paris, 1850, Génération, p. 173.
[2] Zeitschrift der K. K. Gesellschaft der Aerzte, in Wien, 1852.

walls of the uterus, at the time of delivery, are composed of such muscular fibres, arranged in circular, oblique, and longitudinal bundles.

About the end of the first week after delivery, these fibres begin to undergo a fatty degeneration. (Fig. 278.) Their granules become larger and more prominent, and soon assume the appearance of fat granules, deposited in the substance of the fibre. The deposit, thus commenced, increases in abundance, and the granules continue to enlarge until they become converted into fully formed fat globules, which fill the interior of the fibre more or less completely, and mask, to a certain extent, its anatomical characters. (Fig. 279.) The fatty degeneration, thus induced, gives to the uterus a softer consistency, and a pale yellowish color which is characteristic of this period. The altered muscular fibres are afterward absorbed, and gradually give place to others of new formation, which already begin to show themselves before the old ones have disappeared. The process finally results in a complete renovation of the muscular substance of the uterus. The organ becomes again reduced in size, compact in tissue, and of a pale ruddy hue, as in the unimpregnated condition. The entire renewal or reconstruction of the uterus is completed, according to Heschl, about the end of the second month after delivery

Fig. 279.

MUSCULAR FIBRES OF HUMAN UTERUS, three weeks after parturition; from a woman dead of peritonitis.

CHAPTER XIV.

DEVELOPMENT OF THE NERVOUS SYSTEM, ORGANS OF SENSE, SKELETON, AND LIMBS.

THE first trace of the cerebro-spinal axis in the embryo consists of the two longitudinal folds of the external blastodermic layer, which include between them the median furrow, known as the "medullary groove" (page 724). The two folds, after uniting by their corresponding edges on the median line, over the back of the embryo, convert the groove into a canal, the "medullary canal;" and it is within this canal that the cerebro-spinal axis is formed.

Fig. 280.

Formation of the CEREBRO-SPINAL AXIS.—*a*, *b*. Spinal cord. *c*. Cephalic extremity. *d*. Caudal extremity.

The mode of its formation is by the growth of nervous matter upon the inner surface of the medullary canal; and this canal, which becomes the cerebro-spinal canal, is accordingly lined with a secondary internal sheath of nervous matter, which also has the form of a tubular membranous canal, with a continuous central cavity. This is the cerebro-spinal axis, which thus forms a hollow cylindrical cord of nervous matter, running in a longitudinal direction within the cerebro-spinal canal. Anteriorly it expands into a bulbous enlargement corresponding to the brain. Its middle portion, constituting the spinal cord, is nearly cylindrical; and posteriorly, at its caudal extremity, it terminates by a pointed enlargement.

The next change which shows itself is a division of the anterior bulbous enlargement into three secondary compartments or vesicles, partially separated from each other by incomplete transverse constrictions. These are known as the *cerebral vesicles*, from which the different parts of the encephalon are afterward to be developed. The first or most anterior vesicle is destined to form the hemispheres; the second or middle, the tubercula quadrigemina; the third, or posterior, the medulla oblongata. All three vesicles are still hollow, and their cavities communicate freely with each other through the intervening orifices.

Very soon the anterior and posterior cerebral vesicles undergo a further division, the middle one remaining undivided. The anterior vesicle thus separates into two portions, of which the first, or larger, constitutes the hemispheres, while the second, or smaller, becomes the optic

thalami. The third vesicle also separates into two portions, of which the anterior becomes the cerebellum, the posterior the medulla oblongata.

Fig. 281.

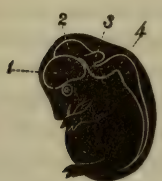
Formation of the CEREBRO-SPINAL AXIS.—1. Vesicle of the hemispheres. 2. Vesicle of the tubercula quadrigemina. 3. Vesicle of the medulla oblongata.

Fig. 282.

FŒTAL PIG, 1¼ centimetre long, showing the condition of the brain and spinal cord.—1. Hemispheres. 2. Tubercula quadrigemina. 3. Cerebellum. 4. Medulla oblongata.

There are, therefore, at this time five cerebral vesicles, all of which communicate with each other and with the central cavity of the spinal cord. The entire cerebro-spinal axis also becomes strongly curved in an anterior direction, corresponding with the anterior curvature of the body of the embryo (Fig. 282); so that the middle vesicle, or that of the tubercula quadrigemina, occupies a prominent angle at the upper part of the encephalon, while the hemispheres and the medulla oblongata are situated below it, anteriorly and posteriorly. At first the relative size of the various parts of the encephalon is very different from that presented in the adult condition. The hemispheres are hardly larger than the tubercula quadrigemina; and the cerebellum is inferior in size to the medulla oblongata. Soon afterward, the relative position and volume of the parts begin to alter. The hemispheres and tubercula quadrigemina grow faster than the posterior portions of the encephalon; and the cerebellum becomes doubled backward over the medulla oblongata. (Fig. 283.) Subse-

Fig. 283.



FŒTAL PIG, three centimetres long.—1. Hemispheres. 2. Tubercula quadrigemina. 3. Cerebellum. 4. Medulla oblongata.

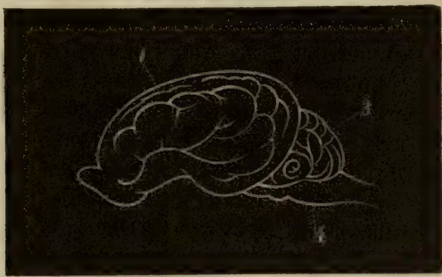
Fig. 284.

HEAD OF FŒTAL PIG, nine centimetres long.—1 Hemispheres. 3. Cerebellum. 4. Medulla oblongata.

quently, the hemispheres enlarge more rapidly, growing upward and backward, so as to cover both the optic thalami and the tubercula

quadrigemina (Fig. 284); the cerebellum tending in the same way to grow backward, and projecting farther in this direction over the medulla oblongata. The subsequent history of the development of the encephalon is mainly a continuation of the same process; the relative dimensions of the parts constantly changing, so that the hemispheres become, in the adult condition (Fig. 285), the largest division of the encephalon.

Fig. 285.



Brain of Adult Pig.—1. Hemispheres. 3. Cerebellum. 4. Medulla oblongata.

while the cerebellum is next in size, and covers the upper portion of the medulla oblongata. The surfaces of the hemispheres and cerebellum, which are at first smooth, become afterward convoluted; thus increasing still farther the extent of their nervous matter. In the human fœtus the cerebral convolutions begin to appear about the beginning of the fifth month (Longet), and grow deeper and more abundant during the remainder of fœtal life.

The lateral portions of the brain growing at the same time more rapidly than that on the median line, they project on each side outward and upward; and by folding over against each other toward the median line, they form the right and left hemispheres, separated by the *longitudinal fissure.* A similar process of growth in the spinal cord results in the formation of its two lateral halves, and the anterior and posterior median fissures of the cord. Elsewhere the median fissure is less complete, as, for example, between the two lateral halves of the cerebellum or those of the medulla oblongata; but it exists everywhere, and marks more or less distinctly the division between the two sides of the nervous centres, produced by the excessive growth of their lateral portions. In this way the whole cerebro-spinal axis is converted into a double organ, equally developed upon the right and left sides, and partially divided by longitudinal median fissures.

Organs of Special Sense.—The eyes are formed by a diverticulum which grows out on each side from the first cerebral vesicle. This diverticulum is at first hollow, its cavity communicating with that of the hemisphere. Afterward, the passage between the two is filled with a deposit of nervous matter, and becomes the *optic nerve.* The globular portion of the diverticulum, which is converted into the globe of the eye, has a thin layer of nervous matter deposited upon its internal sur-

face, which becomes the *retina;* the rest of its cavity being occupied by a gelatinous substance, the *vitreous body.* The crystalline lens is formed in a distinct follicle, which is an offshoot of the integument, and becomes partially imbedded in the anterior portion of the eyeball. The cornea also is originally a part of the integument, and remains somewhat opaque until a late period of development. It becomes nearly transparent a short time before birth.

The iris is a muscular septum, formed in front of the crystalline lens. Its central opening, which afterward becomes the pupil, is at first closed by a vascular membrane, the *pupillary membrane*, passing across the axis of the eye. The bloodvessels of this membrane, which are derived from those of the iris, subsequently become atrophied. They disappear first from its centre, and recede gradually toward its circumference; returning upon themselves in loops, the convexities of which are directed toward the centre. The pupillary membrane itself finally becomes atrophied, following in this retrograde process the direction of its receding bloodvessels, namely, from the centre outward. It has completely disappeared by the end of the seventh month. (Cruveilhier.)

The eyelids are formed by folds of the integument, which project from above and below at the situation of the eyeball. They grow so rapidly during the second and third months that their free margins come in contact and adhere together, so that at that time they cannot be separated without some violence. They remain adherent from this period until the seventh month (Guy), when their margins separate and they become free and movable. In carnivorous animals (dogs and cats), the eyelids do not separate from each other until eight or ten days after birth.

The internal ear is formed in a somewhat similar manner with the eyeball, by an offshoot from the third cerebral vesicle; the passage between them filling up by a deposit of white substance, which becomes the auditory nerve. The tympanum and auditory meatus are both offshoots from the external integument.

Skeleton and Limbs.—At a very early period of development there appears, immediately beneath the medullary canal, a cylindrical cord, termed the *chorda dorsalis* (page 725). It consists of a tubular sheath containing a mass cf simple cells, closely packed together and united by adhesive material. It does not become a permanent part of the skeleton, but is a temporary organ destined to disappear as development proceeds.

On each side of the chorda dorsalis there is formed a series of rectangular plates, the "primitive vertebræ," a portion of whose substance is devoted to the formation of muscular tissue, while another portion becomes the basis for the permanent vertebræ. The latter are deposited in the form of cartilaginous plates, which encircle the chorda dorsalis in a series of rings, corresponding in number with the bodies of the future vertebræ. The rings increase in thickness from without inward, encroaching upon the substance of the chorda dorsalis, and

finally taking its place altogether. The thickened rings, thus solidified by cartilaginous deposit, become the bodies of the vertebræ; while their transverse and articulating processes, with the laminæ and spinous processes, are formed by outgrowths from the bodies in various directions.

When the union of the dorsal plates upon the median line fails to take place, the spinal canal remains open at that situation, and presents the malformation known as *spina bifida.* This may consist simply in a fissure of the spinal canal, more or less extensive, in which case it may sometimes be cured, or may even close spontaneously; or it may be complicated with either an imperfect development or complete absence of the spinal cord at the same spot, producing permanent paralysis of the lower extremities.

The entire skeleton is at first cartilaginous. The first points of ossification show themselves about the beginning of the second month, almost simultaneously in the clavicle and the lower jaw. Then come, in the following order, the femur, humerus, and tibia, the superior maxilla, the bodies of the vertebræ, the ribs, the vault of the cranium, the scapula and the pelvis, the metacarpus and metatarsus, and the phalanges of the fingers and toes. The bones of the carpus are all cartilaginous at birth, and do not begin to ossify until a year afterward. According to Cruveilhier, the calcaneum, the cuboid, and sometimes the astragalus, begin their ossification during the latter periods of fœtal life, but the remainder of the tarsus is cartilaginous at birth. The lower extremity of the femur, according to the same authority, shows a point of ossification at birth; all the other extremities of the long bones being still in a cartilaginous condition at this time. The scaphoid bone of the tarsus and the pisiform bone of the carpus are the last to commence their ossification, several years after birth. Nearly all the bones ossify from several distinct points; the ossification spreading as the cartilage increases in size, and the various bony pieces, thus produced, uniting with each other at a later period, usually some time after birth.

The limbs appear by a budding process, as offshoots of the external blastodermic layer. They are at first mere rounded elevations, without any separation between the fingers and toes, or any distinction between the different articulations. Subsequently the free extremity of each limb becomes divided into the phalanges of the fingers or toes; and afterward the articulations of the wrist and ankle, knee and elbow, shoulder and hip, appear successively from below upward.

The lower limbs in man are less rapid in development than the upper. Both the legs and the pelvis are very slightly developed in the early periods of growth, as compared with the spinal column, to which they are attached. The inferior extremity of the spinal column, formed by the sacrum and coccyx, projects at first beyond the pelvis, forming a tail, which is curled forward toward the adbomen, and terminates in a pointed extremity. The entire lower half of the body, with the spinal column and appendages, is also twisted, from left to right; so that the pelvis is not only curled forward, but also faces at right angles to the

direction of the head and upper part of the body. Subsequently the spinal column becomes straighter and loses its twisted form. At the same time the pelvis and the muscular parts seated upon it grow so much faster than the sacrum and coccyx, that the latter become concealed under the adjoining soft parts, and the rudimentary tail disappears.

Fig. 286.

HUMAN EMBRYO, about one month old. Showing the large size of the head and upper parts of the body; the twisted form of the spinal column; the rudimentary condition of the upper and lower extremities; and the rudimentary tail at the end of the spinal column.

The *integument* of the embryo is at first thin, vascular, and transparent. It afterward becomes thicker, more opaque, and whitish in color. Even at birth, however, it is considerably more vascular than in the adult condition, and its ruddy color, due to its transparency and the abundance of its capillary bloodvessels, is strongly marked. The hairs begin to appear about the middle of intra-uterine life; showing themselves first upon the eyebrows, afterward upon the scalp, trunk and extremities. The nails are in process of formation from the third to the fifth month; and, according to Kölliker, are covered with a layer of epidermis until after the latter period. The sebaceous matter of the cutaneous glandules accumulates upon the skin after the sixth month, and forms a whitish, semi-solid, oleaginous layer, the *vernix caseosa*, which is most abundant in the flexures of the joints, between the folds of the integument, behind the ears, and upon the scalp.

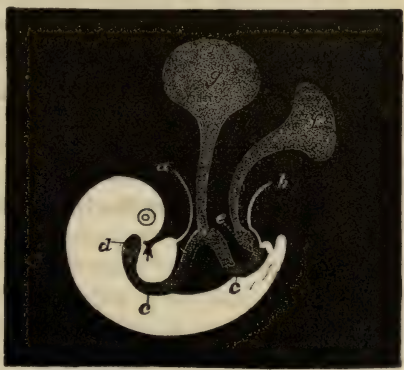
CHAPTER XV.

DEVELOPMENT OF THE ALIMENTARY CANAL AND ITS APPENDAGES.

The intestinal canal is formed, as already described (page 726), from the internal blastodermic layer which curves downward and inward on each side, and is thus converted into a cylindrical tube, terminating at each extremity in a cul-de-sac, and inclosed by the external blastodermic layer. The abdominal walls do not unite with each other upon the median line until after the formation of the intestinal canal; so that, during a certain period, the abdomen of the embryo is widely open in front, presenting a long oval excavation, in which the intestinal tube is situated, running from its anterior to its posterior extremity.

Stomach and Intestine.—The formation of the stomach takes place in the following manner: The alimentary canal, originally straight, soon presents two lateral curvatures at the upper part of the abdomen; the first to the left, the second to the right. The first of these curvatures becomes expanded into a wide sac, projecting laterally from the median line into the left hypochondrium, forming the great pouch of the stomach. The second curvature, directed to the right, marks the boundary between the stomach and the duodenum; and the tube at that point, becoming constricted and furnished with an unusually thick circular layer of muscular fibres, is converted into the pylorus. Immediately below the pylorus, the duodenum turns to the left; and these curvatures, increasing in number and complexity, form the convolutions of the small intestine. The large intestine assumes a spiral curvature; ascending on the right side, then crossing over to the left as the transverse colon, and again descending on the left side, to terminate by the sigmoid flexure in the rectum.

Fig. 287.



Formation of the ALIMENTARY CANAL.—*a, b.* Commencement of amnion. *c, c.* Intestine. *d.* Pharynx. *e.* Urinary bladder. *f* Allantois or chorion. *g.* Umbilical vesicle.

The curvatures of the intestinal canal, which take place in an antero-posterior, as well as in a lateral direction, may be best studied in a profile view, as in Fig. 287. The abdominal walls are here still imperfectly closed,

leaving a wide opening at *a*, *b*, where the integument of the fœtus is continuous with the commencement of the amniotic membrane. The intestine makes at first a single angular turn forward, and opposite the most prominent portion of this angle is to be seen the stem of the umbilical vesicle (*g*). A short distance below this point the intestine subsequently enlarges in calibre, and the situation of this enlargement marks the commencement of the colon. The two portions of the intestine, after this period, become widely different from each other. The upper portion, which is the small intestine, grows most actively in the direction of its length, and becomes a long, narrow, convoluted tube; while the lower portion, which is the large intestine, increases rapidly in diameter, but elongates less than the former. The rectum is the part of the large intestine which alters least its form and position. It elongates comparatively little, retains its position for the most part upon the median line, and as its name indicates, continues to follow a nearly straight course; presenting only a moderate antero-posterior curvature corresponding with the hollow of the sacrum, and a slight lateral obliquity, from its upper portion which is placed a little toward the left, to the anus which is situated upon the median line. At first forming the blind extremity of the large intestine, it subsequently communicates with the exterior by a perforation which becomes the anus. In the chick-embryo, according to Burdach,[1] the perforation of the anus appears on the fifth day of incubation; in the human embryo it is formed during the seventh week. In certain instances, this opening fails to take place, and the rectum is still closed at birth; presenting the malformation known as *imperforate anus.* If the rectum be otherwise fully developed, it may sometimes be felt, distended with meconium, immediately under the integument; and an artificial opening may be successfully made by an incision at the anal region. In other cases, there is also a deficiency, more or less extensive, of the rectum itself, the large intestine terminating in the upper portion of the pelvic cavity.

At the point of junction between the small and the large intestine, a lateral diverticulum of the latter shows itself, and increases in extent, until the ileum seems at last to be inserted obliquely into the side of the colon. The diverticulum of the colon is at first conical in shape; but afterward that portion which forms its free extremity becomes narrow, elongated, and sometimes twisted upon itself, forming the appendix vermiformis; while the remaining portion, which is continuous with the intestine, becomes exceedingly enlarged, and forms the caput coli.

The caput coli and the appendix vermiformis are at first situated near the umbilicus; but between the fourth and fifth months (Cruveilhier) their position is altered, and they become fixed in the right iliac region. During the first six months the internal surface of the small intestine is smooth. At the seventh month, the valvulæ conniventes begin to appear, after which they increase slowly in size, but are still comparatively

[1] Traité de Physiologie, traduit par Jourdan. Paris, 1838, tome iii. pp. 274, 468.

undeveloped at the time of birth. The division of the colon into sacculi by longitudinal and transverse bands, is also an appearance which presents itself only during the last half of fœtal life. Previous to that time, the colon is smooth and cylindrical, like the small intestine.

After the small intestine is formed, it increases rapidly in length. It grows, at this time, faster than the walls of the abdomen; so that it can no longer be contained in the abdominal cavity, but protrudes, under the form of an intestinal loop, or hernia, from the umbilical opening. (Fig. 288.) In the human embryo, this protrusion of the intestine can be readily seen during the latter part of the second month. At a subsequent period, the walls of the abdomen grow more rapidly than the intestine; and, gradually enveloping the hernial protrusion, at last reinclose it in the cavity of the abdomen.

Fig. 288.

FŒTAL PIG, showing the protruding loop of intestine, forming umbilical hernia; from a specimen in the author's possession. From the convexity of the loop a thin filament is seen passing to the umbilical vesicle, which, in the pig, has a flattened, leaf-like form.

Owing to imperfect development of the abdominal walls, and incomplete closure of the umbilicus, the intestinal protrusion, which is normal during the early stages of fœtal life, sometimes remains at birth, and thus produces *congenital umbilical hernia.* As the parts at this time have a natural tendency to unite with each other, if the hernial protrusion be returned within the abdomen, and retained by simple pressure for a sufficient period, the defect is usually remedied, and a permanent cure effected. The conditions are different in a hernia in the adult, where it is due to pressure from within, and a gradual yielding of the fibrous tissues. As the natural period for the closure of the abdominal orifices has passed, the intestine may be retained within the abdomen, in such cases, by mechanical means, but usually escapes again when the pressure is taken off.

The *contents of the intestine*, which accumulate during fœtal life, vary in different parts of the alimentary canal. In the small intestine they are semifluid in consistency, of a light yellowish or grayish-white color in the duodenum, yellow, reddish-brown, and greenish-brown below. In the large intestine they are dark greenish and pasty in consistency; and the contents of this portion of the alimentary canal have received the name of *meconium*, from their resemblance to inspissated poppy-juice. The meconium contains a large quantity of fat, as well as various insoluble substances, probably the residue of epithelial and mucous accumulations. It does not exhibit any trace of the biliary substances proper (taurocholates and glycocholates) when examined by Pettenkofer's test; and cannot therefore be regarded as resulting from the accumulation of bile. In the contents of the small intestine, on the contrary, according to Lehmann, slight traces of bile may be found, as

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early as between the fifth and sixth months. We have found distinct traces of bile in the small intestine at birth, but it is even then in extremely small quantity, and is sometimes altogether absent.

The meconium, therefore, and the intestinal contents generally, are not composed principally, or even to any measurable extent, of the secretions of the liver. They appear rather to be derived from the mucous membrane of the intestine. Even their yellowish and greenish color does not depend on the presence of bile, since the yellow color first shows itself about the middle of the small intestine, and not at its upper extremity. The material which afterward accumulates appears to extend from this point upward and downward, gradually filling the intestine, and becoming, in the ileum and large intestine, darker colored and more pasty as gestation advances.

It is, perhaps, of some importance in this connection, that the amniotic fluid, during the latter half of fœtal life, finds its way, in greater or less abundance, into the stomach, and through that into the intestinal canal. Small cheesy-looking masses are sometimes to be found at birth in the fluid contained in the stomach, which are seen on microscopic examination to be portions of the vernix caseosa exfoliated from the skin into the amniotic cavity, and afterward introduced through the œsophagus into the stomach. According to Kölliker, the downy hairs of the fœtus, exfoliated from the skin, are often swallowed in the same way, and may be found in the meconium.

The *gastric juice* is not secreted before birth; the contents of the stomach being generally in small quantity, clear, nearly colorless, and neutral or alkaline in reaction.

Liver.—The liver is developed at a very early period. Its size in proportion to that of the entire body is much greater in the early months than at birth or in the adult condition. In the fœtal pig we have found the relative size of the liver greatest within the first month, when it amounts to nearly 12 per cent of the entire weight of the body. Afterward it grows less rapidly than other parts, and its relative weight diminishes successively to 10 per cent. and 6 per cent.; being reduced before birth to 3 or 4 per cent. In man, also, the weight of the liver at birth is between 3 and 4 per cent. of that of the entire body.

The *glycogenic function* of the liver commences during fœtal life, and at birth the tissue of the organ is abundantly saccharine. In the early periods of gestation, however, sugar is produced in the fœtus from other sources than the liver. In very young fœtuses of the pig, both the allantoic and amniotic fluids are saccharine a considerable time before glucose makes its appearance in the liver. Even the urine, in half-grown fœtal pigs, contains an appreciable quantity of sugar, and the young animal is normally, at this period, in a diabetic condition. The glucose disappears before birth, as shown by Bernard,[1] from both

[1] Leçons de Physiologie Expérimentale. Paris, 1855, p. 398.

the urine and the amniotic fluid; while the liver begins to produce the saccharine substance which it contains after birth.

Lungs, Thoracic Cavity, and Diaphragm.—The anterior portion of the alimentary canal, which occupies the region of the neck, is the œsophagus. It is straight, and, at first, very short; but it subsequently increases in length, simultaneously with the growth of the neighboring parts. As the œsophagus lengthens, the lungs begin to be developed by a protrusion from the anterior portion of the œsophagus, representing the commencement of the trachea. This protrusion soon divides into two symmetrical branches, which themselves elongate and become repeatedly subdivided, forming the bronchial tubes and their ramifications. At first, the lungs project into the upper part of the abdominal cavity; for there is still no distinction between the chest and abdomen. Afterward, a horizontal partition begins to form on each side, at the level of the base of the lungs, which gradually closes together to form the diaphragm, and which finally shuts off the cavity of the chest from that of the abdomen. Before the closure of the diaphragm is complete, an opening exists by which the peritoneal and pleural cavities communicate with each other. In some instances the development of the diaphragm is arrested at this point, either on one side or the other, and the opening remains permanent. The abdominal organs then partially protrude into the cavity of the chest on that side, forming *congenital diaphragmatic hernia.* The lung on the affected side usually remains in a state of imperfect development. Diaphragmatic hernia of this character is more frequently found upon the left side than upon the right, and may sometimes continue until adult life without causing serious inconvenience.

Urinary Bladder and Urethra.—Soon after the formation of the intestine a vascular outgrowth takes place from its posterior portion, which gradually protrudes from the open walls of the abdomen, until it comes in contact with the external investing membrane of the egg (Fig. 287, *f*); forming subsequently, by its continued growth and expansion, the allantois in the lower animals, the chorion in man.

The chorion, in the portion immediately connected with the body of the embryo, has, like the allantois, the form of a hollow canal; but as it spreads out, to constitute the external investment of the egg, it takes the shape of a continuous membrane, forming the chorion proper (p. 746). The tubular cavity of its connecting portion, the umbilical cord, subsequently becomes obliterated; the obliteration commencing at its outer extremity and gradually proceeding inward until it reaches the umbilicus. Inside the umbilicus it still proceeds for a certain distance and then ceases. Thus the original protrusion of the intestinal canal within the abdomen, which gave rise to the allantois and the chorion, is divided into two portions. The first portion, or that immediately connected with the intestine, remains hollow, and forms afterward the *urinary bladder.* The second portion, between the urinary

bladder and the umbilicus, is consolidated into a rounded cord, which is termed the *urachus.*

The urinary bladder is at first, accordingly, a pyriform sac (Fig. 287, *e*), communicating at its base with the lower portion of the intestinal canal, and continuous by its superior pointed extremity with the solid cord of the urachus, by means of which it is attached to the internal surface of the abdominal walls at the situation of the umbilicus. Afterward, the bladder loses this conical form, and its superior fundus becomes in the adult rounded and bulging.

Development of the Mouth and Face.—The intestinal canal is at first a cylindrical tube, closed at its anterior as well as at its posterior extremity. In the region of the abdomen, which in the earliest periods of development constitutes nearly the whole length of the body, the blastoderm separates, as previously described (p. 735), into two laminæ, an outer and an inner. The outer lamina, consisting of the external integument and the subjacent voluntary muscles, forms the parietes of the abdomen. The inner lamina forms the mucous membrane of the alimentary canal, with its covering of involuntary muscular fibres. Owing to the separation of these two laminæ, there is formed the peritoneal cavity, between the intestine on the one side and the abdominal walls on the other.

But in the anterior part of the body of the embryo, this separation between the two laminæ of the blastoderm does not take place. Consequently, the corresponding portion of the alimentary canal, namely, the œsophagus, remains in contact with the surrounding parts; and its anterior rounded extremity, the pharynx (Fig. 287, *d*), lies immediately underneath the head, covered in front only by the tissues of the external blastodermic layer.

At this time there are formed, on the sides and front of the neck, four nearly transverse fissures, the *cervical fissures*, leading from the exterior into the cavity of the pharynx. These fissures, or clefts, are analogous to those which exist permanently at the same situation in fishes, where the gills are located, and by which the water, taken in at the mouth, is expelled through the sides of the neck. But in the mammalian embryo they have only a temporary existence as continuous openings. The three lower fissures disappear entirely by the subsequent adhesion of their adjacent edges; and in the chick, according to Foster and Balfour, are completely closed by the seventh day of incubation. The upper fissure is converted into a narrow canal, leading from the exterior into the pharynx, but closed about its middle by a transverse partition. The outer portion of this canal becomes the external auditory meatus; the inner portion, the Eustachian tube. The transverse partition is the membrana tympani.

The cervical fissures in man are especially connected with the formation of the mouth and face. Between the fissures there are, of course, bands or ridges of solid tissue, belonging to the external lamina of the blastoderm; and these bands, especially the upper, increase in growth to

such an extent that they become more or less prominent folds, and have received the name of the "visceral folds." The first visceral fold grows rapidly forward, and divides into two somewhat diverging processes or offshoots, which continue to become more and more prominent. The corresponding processes from the right and left sides tend to approach each other, and to unite upon the median line. Those of the lower pair do so unite, and thus form the *inferior maxilla.* Those of the upper pair, which form the *superior maxilla*, unite, not with each other, but with an intervening process which grows from above downward, upon the median line, between them.

By this growth of folds or processes in an anterior direction, and by their union, above and below, upon the median line, there is included between them a depressed space, lined with a continuation of the external blastodermic layer, and situated immediately in front of the extremity of the pharynx. This excavation is the cavity of the *mouth*, inclosed on each side by the processes of the superior and inferior maxillæ, widely open in front, but terminating at its bottom by a blind pit; there being as yet no communication between it and the interior.

Subsequently an opening is formed between the bottom or back part of the mouth and the cavity of the pharynx, by a perforation through the substance of both blastodermic layers at that point. This perforation takes place in the human embryo, according to Burdach,[1] during the sixth week. The opening thus formed marks the situation of the *fauces;* and the alimentary canal is thus made to communicate with the exterior. The lining membrane of the mouth is consequently derived from the external blastodermic layer, is a continuation of the external integument, and the muscles surrounding it are voluntary muscles; while the mucous membrane of the pharynx and œsophagus is derived from the internal blastodermic layer, and is surrounded by involuntary muscles.

Fig. 289.

HUMAN EMBRYO, about one month old: showing the growth of the frontal process downward, and that of the superior and inferior maxillary processes from the side. From a specimen in the author's possession.

The completion of the component parts of the face about the mouth is accomplished by the continuous development of the five buds or processes, above described, which grow together in such a way as to diminish the size of the originally wide oral orifice, and to modify its form in various directions. (Fig. 289.) The process which grows directly downward in the median line from the frontal region, is called the frontal or intermaxillary process, because it afterward contains, in its lower extremity, the intermaxillary bones, with the four upper incisor teeth. The superior maxillary processes, coming from

[1] Traité de Physiologie; traduit par Jourdan. Paris, 1838, tome iii. p. 468.

the sides, unite with the intermaxillary process, to form the upper jaw. In quadrupeds the intermaxillary bones, containing the upper incisor teeth, remain distinct from those of the superior maxilla, the line of demarcation between them being indicated by a suture. In man, as a general rule, they are consolidated with each other, the only permanent suture being that on the median line, between the right and left halves of the upper jaw. According to Geoffroy Saint-Hilaire,[1] a permanent line of suture sometimes remains between the intermaxillary and the superior maxillary bones.

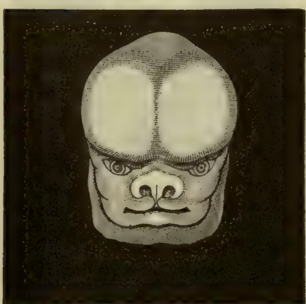
The two inferior maxillary processes unite with each other, making the lower border of the cavity of the mouth, and form, by their union upon the median line, the inferior maxilla. In quadrupeds the two inferior maxillary bones remain permanently divided by a median suture; but in man they are consolidated into a single piece during the first year after birth.

Fig. 290.

HEAD OF HUMAN EMBRYO at about the sixth week. From a specimen in the author's possession.

As the intermaxillary process grows from above downward, it becomes double at its lower extremity, and at the same time gives origin to two lateral offshoots, which curl round and inclose two circular orifices, the anterior nares (Fig. 290); the offshoots themselves becoming the alæ nasi. The external border of the ala nasi subsequently adheres to the superior maxillary process, leaving only a curved crease or furrow at the side of the nose, which marks the line of union between them. In many of the quadrupeds, this furrow remains partially open, extending, as a curvilinear cleft, outward and upward from the orifice of the nostril.

Fig. 291.



HEAD OF HUMAN EMBRYO, about the end of the second month. —From a specimen in the author's possession.

The mouth at this time is wide and gaping, owing to the incomplete development of the upper and lower jaw and the comparative insufficiency of the lips and cheeks. The soft parts afterward increase in growth, and thus gradually diminish the size of the oral orifice (Fig. 291). The lips and cheeks arise by folds of the integument and subjacent muscular layers, which, projecting respectively from above downward, from below upward, and from behind forward, form the permanent borders of the opening of the mouth. The upper lip in man presents a median furrow, bordered by two slightly elevated ridges,

[1] Histoire des Anomalies de l'Organization. Paris, 1832, tome i. p. 581.

corresponding with the union of the superior maxillary and the intermaxillary processes. The lower lip, like the inferior maxilla, is completely consolidated upon the median line, and usually shows no trace of its double origin.

In some instances, the superior maxillary and the intermaxillary processes fail to unite with each other, giving rise to the malformation known as *hare-lip.* The fissure, in cases of hare-lip, is consequently situated, as a general rule, not in the median line, but a little to one side of it, corresponding with the outer edge of the intermaxillary process. Sometimes the same deficiency exists on both sides, forming "double hare-lip;" in which case, if the fissure extend through the bony structures, the central piece of the superior maxilla, detached from the remainder, contains the upper incisor teeth, and corresponds with the intermaxillary bone of the lower animals. In one instance, observed by Wyman,[1] the fissure of hare-lip was situated in the median line, the two intermaxillary bones not having united with each other.

The eyes at an early period are upon the sides of the head (Fig. 289). As development proceeds, they come to be situated farther forward (Fig. 290), their axes being divergent and directed obliquely forward and outward. At a still later period they are placed on the anterior plane of the face (Fig. 291), and have their axes nearly parallel and looking directly forward. This change in situation is effected by the more rapid growth of the posterior and lateral portions of the head, which enlarge in such a manner as to alter the relative position of the parts seated in front.

The palate is formed by a septum between the mouth and nares, which arises on each side as a horizontal offshoot from the superior maxilla. The two plates afterward unite upon the median line, forming a complete partition between the oral and nasal cavities. The right and left nasal passages are separated from each other by a vertical plate (vomer), which grows from above downward and fuses with the palatal plates below. *Fissure of the palate* is caused by a deficiency of one of the horizontal maxillary plates. It is accordingly situated a little on one side of the median line, and is frequently associated with hare-lip and fissure of the upper jaw. The fissures of the palate and of the jaw are often continuous with each other.

The anterior and posterior arches of the palate are incomplete transverse partitions which grow inward from the sides of the fauces, subsequently to the perforation of the pharynx and its communication with the oral cavity. Owing to the muscular tissue which they contain, the orifice of the alimentary canal thus becomes capable of constriction or enlargement, according to its condition of functional activity.

[1] Transactions of the Boston Society for Medical Improvement, March 9th, 1863.

CHAPTER XVI.

DEVELOPMENT OF THE WOLFFIAN BODIES, KIDNEYS, AND INTERNAL ORGANS OF GENERATION.

THE first trace of a urinary apparatus in the embryo consists of two long, fusiform organs, which make their appearance in the abdomen at a very early period, one on each side the spinal column, and which are known by the name of the *Wolffian bodies.* They are fully formed, in the human subject, toward the end of the first month (Coste), at which time they are the largest organs in the abdomen, extending from just below the heart, nearly to the posterior extremity of the body. In the fœtal pig, when thirteen or fourteen millimetres in length, the Wolffian bodies are rounded and kidney-shaped, and occupy a large part of the abdominal cavity. Their combined weight is at this time a little over 3 per cent. of that of the entire body; a proportion which is seven or eight times as large as that of the kidneys in the adult condition. There are, indeed, at this period only three organs of noticeable size in the abdomen, namely, the liver, which has begun to be formed at the upper part of the abdominal cavity; the intestine, which is already somewhat convoluted, and occupies a central position; and the Wolffian bodies, which project on each side the spinal column.

Fig. 292.

FŒTAL PIG, 13 millimetres long; from a specimen in the author's possession.—1. Heart. 2. Anterior limb. 3. Posterior limb. 4. Wolffian body. The abdominal walls have been cut away, in order to show the position of the Wolffian bodies.

The Wolffian bodies, in their intimate structure, closely resemble the adult kidney. They consist of secreting tubules, lined with epithelium, running transversely from the inner to the outer edges of the organs, and terminating at their extremities by rounded dilatations. Into each of these dilated extremities is received a globular coil of capillary bloodvessels, or *glomerulus*, similar to those of the kidney. The tubules of the Wolffian body empty into a common excretory duct, which leaves the organ at its lower extremity, and communicates with the intestinal canal, at the point where the diverticulum of the allantois is given off, and where the urinary bladder is afterward to be situated. The principal distinction in structure, between the Wolffian bodies and the kidneys, consists in the size of the tubules and of their glomeruli; these elements being considerably larger in the Wolffian body than in the kidney. In the fœtal pig, when $3\frac{1}{2}$ or 4 centimetres in length,

at which time both organs coexist, the diameter of the tubules of the Wolffian body is 0.125 millimetre, while in the kidney of the same fœtus, the diameter of the tubules is only 0.034 millimetre. The glomeruli in the Wolffian bodies measure 0.55 millimetre in diameter, while those of the kidney measure only 0.14 millimetre. The Wolffian bodies are therefore urinary organs, so far as regards their anatomical structure, and are sometimes known by the name of the "false kidneys." There is little doubt that they perform, at this early period, a function analogous to that of the kidneys, and separate from the blood of the embryo an excrementitious fluid which is discharged into the cavity of the allantois.

Subsequently, the Wolffian bodies increase for a time in size, though not so rapidly as the other organs. Their relative magnitude consequently diminishes. Still later, they suffer an absolute atrophy, and become gradually less perceptible. In the human embryo, they are hardly to be detected after the end of the second month (Longet), and in the quadrupeds they completely disappear long before birth.

The *kidneys* are formed just behind the Wolffian bodies, and are at first entirely concealed by them in a front view, the kidneys being at this time not more than one-fourth or one-fifth part the size of the Wolffian bodies. (Fig. 293.) The kidneys subsequently enlarging, while the Wolffian bodies diminish, the proportion between the two organs is reversed; and the Wolffian bodies appear as small rounded masses, situated on the anterior surface of the kidneys. (Figs. 294 and 295). The kidneys, during this period, grow more rapidly in an upward than in a downward direction, so that the Wolffian bodies come to be situated near their inferior extremity.

Fig. 293.

FŒTAL PIG, 3½ centimetres long. From a specimen in the author's possession.—1. Wolffian body. 2. Kidney.

The kidneys, during the succeeding periods of fœtal life, become in turn very largely developed in proportion to the rest of the internal organs; attaining a size, in the fœtal pig, equal to more than two per cent. in weight of the entire body. This proportion again diminishes before birth, owing to the increased development of other parts. In the human fœtus at birth, the weight of the two kidneys, taken together, is 6 parts per thousand of that of the entire body.

Internal Organs of Generation.—About the same time that the kidneys are formed behind the Wolffian bodies, two oval-shaped organs make their appearance in front, on the inner side of the Wolffian bodies and between them and the spinal column. These bodies are the internal organs of generation; namely, the testicles in the male, and the ovaries in the female. At first they occupy the same situation and present the same appearance, whether the fœtus is afterward to be male or female. (Fig. 294.)

A short distance above the internal organs of generation there commences, on each side, a narrow tube which runs from above downward along the anterior border of the Wolffian body, immediately in front of, and parallel with the excretory duct of this organ. The two tubes then approach each other below; and, joining upon the median line, empty, together with the ducts of the Wolffian bodies, into the base of the allantois, or what will afterward be the urinary bladder. These tubes serve as the excretory ducts of the internal organs of generation; and will afterward become the *vasa deferentia* in the male, and the *Fallopian tubes* in the female. According to Coste, the vasa deferentia at an early period are disconnected with the testicles; and originate, like the Fallopian tubes, by free extremities, presenting each an open orifice. Afterward the vasa deferentia become adherent to the testicles, and establish a communication with the tubuli seminiferi. In the female, the Fallopian tubes remain permanently disconnected with the ovaries, except by the edge of the fimbriated extremity; which in many of the lower animals becomes closely adherent to the ovary, and envelops it more or less completely in a distinct sac.

Fig. 294.

INTERNAL ORGANS OF GENERATION, in a fœtal pig 7½ centimetres long. From a specimen in the author's possession. —1, 1. Kidneys. 2, 2. Wolffian bodies. 3, 3 Internal organs of generation; testicles or ovaries. 4 Urinary bladder turned over in front. 5. Intestine.

Male Organs of Generation; Descent of the Testicles.—In the male fœtus there now commences a change of place in the internal organs of generation, which is known as the "descent of the testicles." In consequence of this change, the testicles, which are at first placed near the middle of the abdomen and in front of the kidneys, come at last to be situated in the scrotum, outside and below the abdominal cavity. They also become inclosed in a distinct serous sac, the tunica vaginalis testis. This apparent movement of the testicles is accomplished in the same manner as that of the Wolffian bodies, namely, by a disproportionate growth of the middle and upper portions of the abdomen and of the tissues above the testicles, so that the relative position of the organs becomes altered.

By the upward enlargement of the kidneys, both the Wolffian bodies and the testicles are soon found to occupy an inferior position. (Fig. 295.) At the same time, a slender rounded cord (not represented in the figure) passes from the lower extremity of each testicle in an outward and downward direction, crossing the vas deferens a short distance above its union with its fellow of the opposite side. Below this point, the cord spoken of continues to run obliquely outward and downward; and, passing through the abdominal walls at the situation of the inguinal canal, is inserted into the subcutaneous tissue near the symphysis pubis. The lower part of this cord becomes the *gubernaculum testis*. It con-

tains muscular fibres, which may be easily detected, in the human fœtus, during the latter half of intra-uterine life. At the period of birth, however, or soon afterward, they have usually disappeared.

Fig. 295.

INTERNAL ORGANS OF GENERATION in a fœtal pig nearly 10 centimetres long. From a specimen in the author's possession.—1, 1. Kidneys. 2, 2. Wolffian bodies. 3, 3. Testicles. 4. Urinary bladder. 5. Intestine.

That portion of the excretory tube of the testicle which is situated outside the crossing of the gubernaculum, is destined to become afterward convoluted, and converted into the *epididymis.* That which is situated inside the same point remains comparatively straight, but becomes considerably elongated, and is finally known as the *vas deferens.*

As the testicles descend still farther in the abdomen, they continue to grow, while the Wolffian bodies, on the contrary, become smaller; and at last, when the testicles have arrived at the internal inguinal ring, the Wolffian bodies have altogether disappeared, or have become so altered that they are no longer recognizable. In the human fœtus, the testicles reach the internal inguinal ring about the termination of the sixth month (Wilson).

During the succeeding month, a protrusion of the peritoneum takes place through the inguinal canal, in advance of the testicle; the last-named organ still continuing its descent. As it passes into the scrotum, loops of muscular fibres are given off from the lower border of the internal oblique muscle of the abdomen, extending downward with the testicle, upon it and upon the elongating spermatic cord. These constitute afterward the *cremaster muscle.*

At last, the testicles descend quite to the bottom of the scrotum. The convoluted portion of the efferent duct, namely, the epididymis, remains attached to the body of the testicle; while the vas deferens passes upward, in a reverse direction, enters the abdomen through the inguinal canal, again bends downward, and joins its fellow of the opposite side; after which they both open into the prostatic portion of the urethra by distinct orifices, situated on either side of the median line. At the same time, two diverticula arise from the median portion of the vasa deferentia, and, elongating in a backward direction, beneath the base of the bladder, become developed into sacculated reservoirs, the *vesiculæ seminales.*

The left testicle is a littler later in its descent than the right; but it afterward passes farther into the scrotum, and, in the adult condition, usually hangs a little lower than the corresponding organ on the opposite side.

After the testicle has passed into the scrotum, the serous pouch,

which preceded its descent, remains for a time in communication with the peritoneal cavity. In many of the quadrupeds, as, for example, the rabbit, this condition is permanent; and the testicle may be alternately drawn downward into the scrotum, or retracted into the abdomen, by the action of the gubernaculum and the cremaster muscle. In the human fœtus, the two opposite surfaces of the peritoneal pouch approach each other at the inguinal canal, forming at that point a constriction, which partly shuts off the testicle from the cavity of the abdomen. By a continuation of this process, the serous surfaces come in contact, and, adhering together at this situation (Fig. 296, 4), form a kind of cicatrix, by which the cavity of the tunica vaginalis (2) is shut off from the general cavity of the peritoneum (3). The tunica vaginalis testis is, therefore, originally a part of the peritoneum, from which it is subsequently separated by the adhesion of its opposite walls.

Fig. 296.

Formation of the TUNICA VAGINALIS TESTIS.—1. Testicle nearly at the bottom of the scrotum. 2. Cavity of tunica vaginalis. 3. Cavity of peritoneum. 4. Obliterated neck of peritoneal sac.

The separation of the tunica vaginalis testis from the peritoneum is usually completed in the human fœtus before birth. But sometimes it fails to take place at the usual time, and the intestine is then liable to protrude into the scrotum, in front of the spermatic cord, giving rise to *congenital inguinal hernia.* (Fig. 297.) The parts implicated in this malformation have still, as in the case of congenital umbilical hernia, a tendency to unite with each other and obliterate the opening; and if the intestine be retained by pressure in the cavity of the abdomen, cicatrization usually takes place at the inguinal canal, and a cure is effected.

Fig. 297.

CONGENITAL INGUINAL HERNIA.—1. Testicle. 2, 2, 2. Intestine.

Female Organs of Generation.—At an early period of development, the ovaries have the same external appearance, and occupy the same position in the abdomen, as the testicles in the opposite sex. The descent of the ovaries also takes place, to a great extent, in the same manner with the corresponding change of position of the testicles. When, in the early part of this descent, they have reached the level of the lower edge of the kidneys, a cord, analogous to the gubernaculum, may be seen proceeding from their lower extremity, crossing the efferent duct on each side, and passing downward, to be attached to the subcutaneous tissues at the situation of the inguinal ring. That part of the duct situated outside the crossing of this cord, becomes convoluted, and is converted into the *Fallopian tube;* while

that which is inside the same point, is developed into the *uterus.* The upper portion of the cord itself becomes the *ligament of the ovary;* its lower portion, the *round ligament of the uterus.*

As the ovaries continue their descent, they pass below and behind the Fallopian tubes, which perform at the same time a movement of rotation, from before backward and from above downward; the whole, together with the ligaments of the ovaries and the round ligaments, being enveloped in double folds of peritoneum, which enlarge with the growth of the parts included between them, and constitute finally the *broad ligaments of the uterus.*

While these changes are taking place in the adjacent organs, the two lateral halves of the uterus fuse with each other upon the median line, and become covered with an abundant layer of muscular fibres. In the quadrupeds, the uterus remains divided at its upper portion, running out into two long conical tubes or cornua (Fig. 228), presenting the form known as the *uterus bicornis.* In the human species, the fusion of the two lateral halves of the organ is nearly complete; so that the uterus presents externally a somewhat rounded, flattened and triangular figure (Fig. 229), with the ligaments of the ovary and the round ligaments passing off from its superior angles. Internally, the cavity of the organ still presents a strongly marked triangular form, the vestige of its original division.

Occasionally the human uterus in the adult condition remains divided by a vertical septum, running from the middle of its fundus downward toward the os internum. The organ may even present a partial external division, corresponding with the situation of the internal septum, and producing the malformation known as "uterus bicornis," or double uterus.

The os internum and the os externum are produced by partial constrictions of the original generative passage; and the anatomical distinctions between the body of the uterus, the cervix, and the vagina, arise from the different modes of development of the mucous membrane and muscular tunic in its corresponding portions. During fœtal life, the neck of the uterus grows faster than its body; so that, at the period of birth, the organ is far from presenting the form which it exhibits in the adult condition. In the human fœtus at term, the cervix uteri constitutes nearly two-thirds of the entire length of the organ; while the body forms but little over one-third. The cervix, at this time, is larger in diameter than the body; so that the whole organ presents a tapering form from below upward. The arbor vitæ uterina of the cervix is at birth very fully developed, and the mucous membrane of the body is also thrown into three or four folds which radiate upward from the os internum. The cavity of the cervix is filled with transparent semi-solid mucus.

The position of the uterus at birth is different from that which it assumes in adult life; nearly the entire length of the organ being above the level of the symphysis pubis, and its inferior extremity passing

below that point only by about six millimetres. It is also slightly anteflexed at the junction of the body and cervix. After birth, the uterus, together with its appendages, continues to descend; and at the period of puberty its fundus is situated just below the level of the symphysis pubis.

The *ovaries* at birth are narrow and elongated in form. They contain at this time an abundance of eggs; each inclosed in a Graafian follicle, and averaging .04 millimetre in diameter. The vitellus is imperfectly formed in most of them, and in some is hardly to be distinguished. The Graafian follicle at this period envelops each egg closely, there being no fluid between its internal surface and the exterior of the egg, but only the thin layer of cells forming the "membrana granulosa." Inside this layer is to be seen the germinative vesicle, with the germinative spot, surrounded by a faintly granular vitellus, more or less abundant in different parts. Some of the Graafian follicles containing eggs are as large as .05 millimetre; others as small as .02 millimetre. In the very smallest, the cells of the membrana granulosa appear to fill entirely the cavity of the follicle, concealing the rudiments of the primitive egg.

CHAPTER XVII.

DEVELOPMENT OF THE VASCULAR SYSTEM.

THERE are three distinct forms assumed by the circulatory system during different periods of life. These different forms of the circulation are connected with the manner in which nutrition and the renovation of the blood are accomplished at different epochs; and they follow each other in the progress of development, as different organs are employed in turn to accomplish the above functions. The first form is that of the *vitelline circulation*, which exists at a period when the vitellus is the source of nutrition for the embryo. The second is the *placental circulation*, which lasts, in man and the mammalians, through the greater part of fœtal life, and is characterized by the existence of the placenta; the third is the complete or *adult circulation*, in which the renovation and nutrition of the blood are provided for by the lungs and the intestinal canal.

Vitelline Circulation.—When the body of the embryo has begun to be formed in the centre of the blastoderm, a number of bloodvessels shoot out from its sides and ramify over the neighboring parts of the vitelline sac, forming by their inosculation an abundant vascular plexus. The area occupied by this plexus around the fœtus is the "area vasculosa." In the egg of the fish (Fig. 298), the area vasculosa occupies the whole surface of the vitellus, outside the body of the embryo. A number of arteries pass out from each side, supplying the vascular network; and the blood is returned from it to the embryo by a principal vein which is seen passing upward along the front of the egg, and entering the body beneath the head.

Fig. 298.

EGG OF FISH (Jarrabacca), showing the vitelline circulation.

In the egg of the fowl, the area vasculosa spreads gradually over the vitelline sac from within outward. It is at first limited on its external border by a terminal vein or sinus, which collects the greater part of the blood from the vascular plexus on each side, and returns it to the interior of the embryo by a double or single trunk, entering, as in the fish, beneath the head. Another vein, of smaller size, enters the body of the embryo near its posterior extremity; and a number of others, still smaller, along the sides. All these vessels gradually change in relative importance, as the development of the embryo proceeds. Especially the terminal sinus becomes less distinct as the area vasculosa extends farther over the vitelline sac, and the anterior and pos-

terior venous trunks disappear more or less completely, to be replaced in importance by some of those which enter upon the sides. The area vasculosa is therefore an appendage to the circulatory apparatus of the embryo, spread out over the surface of the vitellus, and absorbing from it the requisite materials for nutrition.

In man and the mammalians, the first formation of the area vasculosa is not essentially different from that presented in fishes and birds. But owing to the small size and rapid exhaustion of the vitellus as a source of nourishment, this form of the circulation never acquires a high degree of development, and soon becomes retrograde. It presents, however, certain modifications, which are of importance as indicating the mode of origin of various parts of the permanent vascular system.

These modifications relate mainly to the arrangement of the arteries and veins distributing the blood to the external vascular plexus, and returning it thence to the body of the embryo. As the embryo and the entire egg increase in size, there are two arteries and two veins which become larger than the others, and which subsequently do the whole work of conveying the blood to and from the area vasculosa. The two arteries emerge from the lateral edges of the embryo, on the right and left sides; while the two veins enter at about the same point and nearly parallel with them. These four vessels are termed the *omphalo-mesenteric arteries and veins.*

The arrangement of the circulatory apparatus in the interior of the body at this time is as follows: The heart is situated at the median line, immediately beneath the head, and in front of the œsophagus. It receives at its lower extremity the united trunks of the two omphalo-mesenteric veins, and at its upper extremity gives off two vessels which almost immediately divide into two sets of lateral arches, bending backward along the sides of the neck, and again uniting into two trunks near the anterior surface of the vertebral column. These trunks then run from above downward, in a nearly similar direction, on each side the median line. They are called the *vertebral arteries*, on account of their situation, which is parallel with that of the vertebral column. They give off, throughout their course, small lateral branches, which supply the body of the fœtus, and also two larger branches — the omphalo-mesenteric arteries—which pass out, as above described, into the area vasculosa. The two vertebral arteries remain separate in the upper part of the body, but fuse with each other a little beneath the level of the heart; so that, below this point, there remains but one large artery, the aorta, running from above downward along the median line, giving off the omphalo-mesenteric arteries to the area vasculosa, and supplying smaller branches to the body, the walls of the intestine, and the other organs of the embryo.

This is the condition which marks the first or vitelline circulation. A change now begins to be established, by which the vitellus is superseded, as an organ of nutrition, by the placenta; and the second or *placental* circulation takes its place.

Placental Circulation.—After the umbilical vesicle has been formed by the process already described (page 738), a part of the vitellus remains included in it, while the rest is retained in the abdomen and inclosed in the intestinal canal. As these two organs (umbilical vesicle and intestine) are originally parts of the same vitelline sac, they remain supplied by the same vascular system, namely, the omphalo-mesenteric vessels. Those which remain within the abdomen of the fœtus supply the mesentery and intestine; but the larger trunks pass outward, and ramify upon the walls of the umbilical vesicle. (Fig. 299.) At first there are, as above mentioned, two omphalo-mesenteric arteries emerging from the body, and two omphalo-mesenteric veins returning to it; but afterward the two arteries are replaced by a common trunk, while a similar change takes place in the two veins. Subsequently, therefore, there remains but a single artery and a single vein, connecting the internal and external portions of the vitelline circulation.

Fig. 299.

Diagram of the YOUNG EMBRYO AND ITS VESSELS, showing the circulation of the umbilical vesicle, and also that of the allantois, beginning to be formed.

The vessels belonging to this system are called the omphalo-mesenteric vessels, because a part of them (omphalic vessels) pass outward, by the umbilicus, or "omphalos," to the umbilical vesicle, while the remainder (mesenteric vessels) ramify upon the mesentery and the intestine.

At first, the circulation of the umbilical vesicle is more important than that of the intestine; and the omphalic artery and vein appear accordingly as large trunks, of which the mesenteric vessels are small branches. (Fig. 299.) Afterward the intestine enlarges, while the umbilical vesicle diminishes; and the proportion between the two sets of vessels is therefore reversed. The mesenteric vessels then come to be the principal trunks, while the omphalic vessels are minute branches, running out along the stem of the umbilical vesicle, and ramifying in a few scanty twigs upon its surface. (Fig. 300).

In the mean time, the allantois is formed by a protrusion from the lower extremity of the intestine, which, carrying with it two arteries and two veins, passes out by the anterior opening of the body, and comes in contact with the external membrane of the egg. The arteries of the allantois, termed the *umbilical arteries*, are supplied by branches of the abdominal aorta; the umbilical veins, on the other hand, join the mesenteric veins, and empty with them into the venous extremity of the heart. As the umbilical vesicle diminishes, the allantois enlarges; and the latter is converted, in the human subject, into a vascular chorion, part of

which is devoted to the formation of the placenta. (Fig. 300.) As the placenta soon becomes the only source of nutrition for the fœtus, its vessels increase in size, and preponderate over all the other parts of the circulatory system. During the early periods of the formation of the

Fig. 300.

Diagram of the EMBRYO AND ITS VESSELS; showing the second or placental circulation. The intestine has become further developed, and the mesenteric arteries have enlarged, while the umbilical vesicle and its vascular branches are reduced in size. The large umbilical arteries are seen passing out to the placenta.

placenta, there are, as above mentioned, two umbilical arteries and two umbilical veins. Subsequently one of the veins disappears, and the whole of the blood is returned to the fœtus by the other, which becomes enlarged in proportion. For a long time previous to birth, there are, therefore, in the umbilical cord two umbilical arteries, and but one umbilical vein.

Adult Circulation.—The placental circulation is exchanged, at the period of birth, for the third or adult circulation. This is distinguished by the disappearance of the placenta and the vessels connected with it, and by the entrance into activity of the lungs and the alimentary canal, as the organs of nutrition and aeration for the blood. A large proportion of the blood is accordingly turned into different channels, and is distributed to organs which were before but scantily supplied. This change differs from that which preceded it mainly in its suddenness. The transition from the first to the second form of circulation is a gradual one; the vitellus and umbilical vesicle diminishing as the placenta enlarges, and the two organs, with their bloodvessels, coexisting

for a certain period. But at the time of birth the placenta is detached, and the lungs brought into play, with comparative suddenness; and although the pulmonary circulation and respiration are not established in full activity until an interval of some days has elapsed, yet the placenta is at once withdrawn from the circulatory system, and its office is assumed by the lungs, the skin, and the alimentary canal.

The comparatively sudden changes which take place at birth have, however, been already provided for by the gradual development of the necessary organs. This is accompanied by corresponding alterations in both the arterial and venous systems.

Development of the Arterial System.—At an early period of development, the main arterial trunks, after passing off from the anterior extremity of the heart, curve backward in two sets of nearly parallel branches, toward the vertebral column, after which they again become longitudinal, and receive the name of the "vertebral arteries." The curved branches which pass along the sides of the neck, from front to rear, are called the *cervical arches.* They run in the substance of the visceral folds existing in this situation (page 781), and are separated from each other by the intervening cervical fissures. In the chick-embryo, according to Foster and Balfour, three cervical arches, in the three upper visceral folds, have been formed by the end of the second day of incubation. During the third and fourth days, the first and second cervical arches become obliterated, but a fourth and a fifth become developed at the same time, in the substance of the corresponding visceral folds. Thus there are, in all, five vascular cervical arches; but only three are to be found coexisting at any one time.

In fishes, the cervical arches remain, as permanent bloodvessels supplying the gills, generally four in number on each side, sometimes five. In birds and mammalians, some of them disappear during the further progress of development, or leave only certain arterial inosculations in the adult, as vestiges of their existence during the embryonic condition. Some of them, on the other hand, remain as permanent vascular trunks or branches, forming important parts of the adult arterial system.

The details relating to the growth and subsequent modification of the cervical arches are not all described in the same manner by different observers; and there seems to be some variation, in this respect, in the mammalian embryo, as compared with that of birds. The general features, however, of the process of transformation are as follows.

The two ascending trunks, on the anterior part of the neck, from which the cervical arches are given off, become the carotid arteries. The first and second, that is, the two upper cervical arches, on each side, disappear as above mentioned, or remain only in the form of small and inconstant arterial inosculations. The third arch becomes the subclavian artery, giving off, in an upward direction, the permanent vertebral artery, and continuing outward as the axillary artery, to supply the upper limb. The fourth cervical arch undergoes very different changes on the two opposite sides. On the left side it becomes enor-

mously enlarged, giving off, as secondary branches, all the arterial trunks going to the head and upper limbs, and is thus converted into the permanent *arch of the aorta*. On the right side the corresponding arch grows smaller, and ultimately disappears; so that at last there is only a single aortic arch, situated to the left of the median line, and continuous below with the thoracic aorta.

The fifth or last cervical arch becomes on each side the pulmonary artery; its external portion on the right side disappearing at a very early period, but on the left remaining for a certain time, as the ductus arteriosus, between the pulmonary artery and the aorta.

Notwithstanding that the cervical arches are at first, as their name implies, all situated in the region of the neck, their remains or permanent representatives in the complete form of the arterial system, come to be placed farther downward, and are even found in the cavity of the chest. This is due to the varying rapidity of growth in different parts, at the successive periods of embryonic development. The thorax at first has no existence as a distinct portion of the trunk; the heart being placed immediately beneath the head, and afterward changing its relative position as the development of the lungs goes forward and the walls of the chest expand to cover them. The neck, with the œsophagus and trachea, also elongates in an upward direction, so that the vascular organs at first placed in the cervical region afterward occupy a position lower down. In fishes, where the cervical arches are permanent and where no lungs are developed, there is no thoracic cavity, and the heart remains situated at the most anterior portion of the trunk, just behind the gills.

Corresponding changes take place, during this time, in the lower part of the body. Here the abdominal aorta runs undivided, upon the median line, quite to the end of the spinal column; giving off on each side lateral branches, which supply the intestine and the parietes of the body. When the allantois begins to be developed, two of these lateral branches accompany it, and become, consequently, the umbilical arteries. These vessels increase so rapidly in size, that they soon appear as divisions of the aortic trunk; while the original continuation of the aorta, running to the end of the spinal column, appears as a small branch given off at the point of bifurcation. The lower limbs are supplied by two small branches, given off from the umbilical arteries near their origin.

Up to this time, the pelvis and posterior extremities are but slightly developed. Subsequently they grow more rapidly, in proportion to the rest of the body, and the arteries which supply them enlarge in a corresponding manner. That portion of the umbilical arteries, lying between the bifurcation of the aorta and the origin of the branches going to the lower extremities, becomes the common iliac arteries, which in their turn afterward divide into the umbilical arteries proper, and the femorals. Subsequently, in accordance with the continued growth of the pelvis and lower extremities, the relative size of their bloodvessels is still

further increased; and at last the arterial system in this part of the body assumes the arrangement which belongs to the latter periods of gestation. The aorta divides, as before, into the two common iliac arteries. These divide into the external iliacs supplying the lower extremities, and the internal iliacs supplying the pelvis; and this division is so placed that the umbilical or hypogastric arteries arise from the internal iliacs, of which they now appear to be secondary branches.

After the birth of the fœtus and the separation of the placenta, the hypogastric arteries become partially atrophied, and are converted, in the adult condition, into solid cords, running upward to the umbilicus. Their lower portion, however, remains pervious, and gives off arteries supplying the urinary bladder. The terminal continuation of the original abdominal aorta, is the arteria sacra media, which, in the adult, runs downward on the anterior surface of the sacrum, supplying branches to the rectum and to the anterior sacral nerves.

Fig. 301.

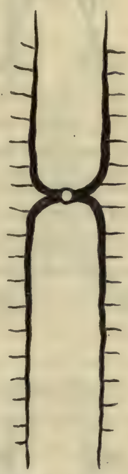


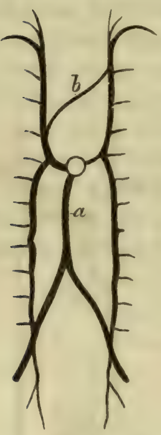
Diagram of the VENOUS SYSTEM in its early condition; showing the vertebral veins emptying into the heart by two lateral trunks, the "canals of Cuvier."

Development of the Venous System.—According to the observations of Coste, the principal veins of the body consist at first of two long venous trunks, the *vertebral veins* (Fig. 301), which run along the sides of the vertebral column, parallel with the vertebral arteries. They receive in succession all the intercostal veins, and empty into the heart by two lateral trunks of equal size, the *canals of Cuvier*. When the inferior extremities become developed, their two veins, returning from below, join the vertebral veins near the posterior portion of the body; and, crossing them, afterward unite with each other, thus constituting another vein of new formation (Fig. 302, a), which runs upward a little to the right of the median line, and empties by itself into the lower extremity of the heart.

The two branches, by means of which the veins of the lower extremities thus unite, become afterward the common iliac veins; while the single trunk (a) resulting from their union becomes the *vena cava inferior*. Subsequently, the vena cava inferior becomes very much larger than the vertebral veins; and its two branches of bifurcation are afterward represented by the iliac veins.

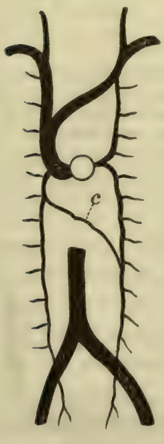
Above the level of the heart, the vertebral and intercostal veins retain their relative size until the development of the superior extremities has commenced. Then, two of the intercostal veins increase in diameter (Fig. 302), and become converted into the right and left subclavians; while those portions of the vertebral veins situated above the subclavians become the right and left jugular veins. Just below the junction of the jugulars with the subclavians, a small branch of communication now appears between the two vertebrals (Fig. 302, b), passing over from

Fig. 302.



VENOUS SYSTEM farther advanced, showing the formation of the iliac and subclavian veins —*a*. Vein of new formation, which becomes the inferior vena cava. *b*. Transverse branch of new formation, which afterward becomes the left vena innominata.

Fig. 303.



Further development of the VENOUS SYSTEM.—The vertebral veins are much diminished in size, and the canal of Cuvier, on the left side, is gradually disappearing. *c*. Transverse branch of new formation, which is to become the vena azygos minor.

left to right, and emptying into the right vertebral vein a little above the level of the heart; so that a part of the blood coming from the left side of the head, and the left upper extremity, still passes down the left vertebral vein to the heart upon its own side, while a part crosses over by the communicating branch (*b*), and is finally conveyed to the heart by the right descending vertebral. Soon afterward, this branch of communication enlarges so rapidly that it preponderates over the left superior vertebral vein, from which it originated (Fig. 303), and, serving then to convey all the blood from the left side of the head and left upper extremity to the right side above the heart, it becomes the left *vena innominata*.

On the left side, that portion of the superior vertebral vein, which is below the subclavian, remains as a small branch of the vena innominata, receiving the six or seven upper intercostal veins; while on the right side it becomes excessively enlarged, receiving the blood of both jugulars and both subclavians, and is converted into the *vena cava superior*.

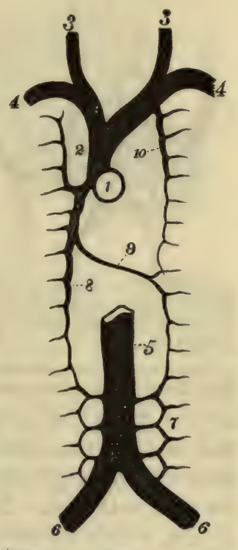
The left canal of Cuvier, by which the left vertebral vein at first communicates with the heart, is subsequently atrophied and obliterated, while on the right side it becomes excessively enlarged, and forms the lower extremity of the vena cava superior.

The superior and inferior venæ cavæ, accordingly, do not correspond with each other so far as regards their mode of origin, and are not to be regarded as analogous veins. The superior vena cava is one of the original vertebral veins; while the inferior vena cava is a vessel of new formation, resulting from the union of two lateral trunks coming from the inferior extremities.

The remainder of the vertebral veins finally assume the condition shown in Fig. 304, which is the complete or adult form of the venous circulation. At the lower part of the abdomen, the vertebral veins send inward small transverse branches of communication to the vena cava inferior, between the points at which they receive the intercostal veins. These

branches of communication, by increasing in size, become the *lumbar veins* (7), which, in the adult condition, communicate with each other by arched branches, a short distance to the side of the vena cava. Above the level of the lumbar arches, the vertebral veins retain their original direction. That upon the right side still receives all the right intercostal veins, and becomes the *vena azygos major* (8). It also receives a small branch of communication from its fellow of the left side (Fig. 303, *c*), and this branch soon enlarges to such an extent as to bring over to the vena azygos major all the blood of the five or six lower intercostal veins of the left side, becoming, in this way, the *vena azygos minor* (9). The six or seven upper intercostal veins on the left side still empty, as before, into their own vertebral vein (10), which, joining the left vena innominata above, is known as the *superior intercostal vein.* The left canal of Cuvier has by this time entirely disappeared; so that all the venous blood now enters the heart by the superior and the inferior vena cava. But the original vertebral veins are still continuous throughout, though much diminished in size at certain points; since both the greater and lesser azygous veins inosculate below with the superior lumbar veins, and the superior intercostal vein inosculates below with the lesser azygous, before it crosses to the right side.

Fig. 304.



Adult condition of the Venous System.—1. Right auricle of the heart. 2. Vena cava superior. 3, 3. Jugular veins. 4, 4. Subclavian veins. 5. Vena cava inferior. 6, 6. Iliac veins. 7. Lumbar veins. 8. Vena azygos major. 9. Vena azygos minor. 10. Superior intercostal vein.

There are still two parts of the circulatory apparatus, the development of which presents peculiarities sufficiently important to be described separately. These are, first, the liver and the ductus venosus, and secondly, the heart and ductus arteriosus.

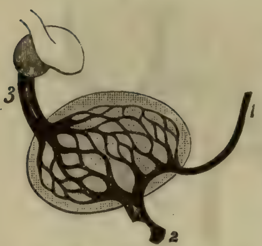
The Hepatic Circulation and Ductus Venosus.—The liver appears at a very early period, in the upper part of the abdomen, as a mass of glandular and vascular tissue, developed around the upper portion of the omphalo-mesenteric vein, just below its termination in the heart (Fig. 305). As soon as the organ has attained a considerable size, the omphalo-mesenteric vein (1) breaks up in its interior into a capillary plexus, the vessels of which again unite into a venous trunk, which conveys the blood to the heart. The omphalo-mesenteric vein

Fig. 305.

Early form of the Hepatic Circulation.—1. Omphalo-mesenteric vein. 2. Hepatic vein. 3. Heart. The dotted line shows the situation of the future umbilical vein.

below the liver then becomes the *portal vein;* while above the liver, and between that organ and the heart, it receives the name of the *hepatic vein* (2). The liver, accordingly, is at this time supplied with blood entirely by the portal vein, coming from the umbilical vesicle and the intestine; and all the blood derived from this source passes through the hepatic circulation before reaching the venous extremity of the heart.

Fig. 306.



HEPATIC CIRCULATION farther advanced. — 1. Portal vein. 2 Umbilical vein. 3. Hepatic vein.

But soon afterward the allantois makes its appearance, and becomes developed into the placenta; and the umbilical vein returning from it joins the omphalo-mesenteric vein in the substance of the liver, and takes part in the formation of the hepatic capillary plexus. Since the umbilical vesicle, however, becomes atrophied, while the intestine remains inactive, at the same time that the placenta increases in size and in functional importance, a period arrives when the liver receives more blood by the umbilical vein than by the portal vein. (Fig. 306.) The umbilical vein then passes into the liver at the longitudinal fissure, and supplies the left lobe entirely with its own branches. To the right it sends off a large branch of communication, which opens into the portal vein, and partially supplies the right lobe with umbilical blood. The liver is thus supplied with blood from two different sources, the most abundant of which is the umbilical vein; and all the blood entering the liver circulates, as before, through its capillary vessels.

But the liver is much larger, in proportion to the entire body, at an early period of fœtal life than in the later months. In the fœtal pig, when very young, it amounts to nearly twelve per cent. of the weight of the whole body; while before birth it diminishes to seven, six, and even three or four per cent. For some time, therefore, during the latter part of fœtal life, much more blood returns from the placenta than is required for the capillary circulation of the liver. Accordingly, a vascular duct or canal is formed in its interior, by which a portion of the placental blood is carried directly through the organ, and conveyed to the heart without having passed through the hepatic capillaries. This canal is the *Ductus venosus.*

The ductus venosus is formed by a gradual dilatation of one of the hepatic capillaries (at 5 Fig. 307), which, enlarging excessively, becomes converted into a wide branch of communication, passing from the umbilical vein below to the hepatic vein above. The circulation through the liver, at this period, is as follows: A certain quantity of venous blood still enters through the portal vein (1), and circulates in a part of the capillary system of the right lobe. The umbilical vein (2), bringing a much larger quantity of blood, enters the liver a little to the left, and the blood which it contains divides into three principal streams. One of

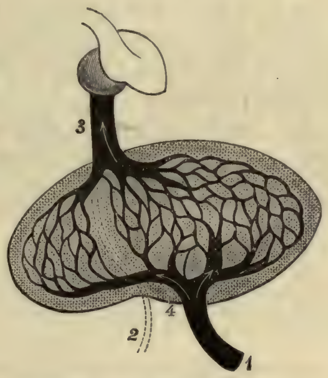
them passes through the left branch (3) into the capillaries of the left lobe; another turns off through the right branch (4), and, joining the blood of the portal vein, circulates through the capillaries of the right lobe; while the third passes directly onward through the ductus venosus (5) and reaches the hepatic vein without having passed through any part of the capillary plexus.

Fig. 307.

HEPATIC CIRCULATION during the latter part of fœtal life.—1. Portal vein. 2. Umbilical vein. 3 Left branch of umbilical vein. 4. Right branch of umbilical vein. 5. Ductus venosus. 6. Hepatic vein.

This condition of the hepatic circulation continues until birth. At that time, two important changes take place. First, the placental circulation is cut off; and secondly, a much larger quantity of blood than before begins to circulate through the vessels of the lungs and the intestine. The superabundance of blood, previously coming from the placenta, is now diverted to the lungs; while the intestinal canal becomes the sole source of supply for the hepatic venous blood. The following changes, therefore, take place at birth in the vessels of the liver. (Fig. 308.) First, the umbilical vein shrivels and becomes converted into a solid cord (2). This cord may be seen, in the adult condition, running from the internal surface of the abdominal walls, at the umbilicus, to the longitudinal fissure of the liver. It is then known under the name of the *round ligament.* Secondly, the ductus venosus also becomes obliterated. Thirdly, the blood entering the liver by the portal vein (1) passes off by its right branch, as before, to the right lobe. But in the left branch (4) the course of the blood is reversed. This was formerly the right branch of the umbilical vein, its blood passing in a direction from left to right. It now becomes the left branch of the portal vein; and its blood passes from right to left, to be distributed to the capillary vessels of the left lobe.

Fig. 308.



Adult form of HEPATIC CIRCULATION.—1. Portal vein. 2. Obliterated umbilical vein, forming the round ligament; the continuation of the dotted lines through the liver shows the situation of the obliterated ductus venosus. 3. Hepatic vein. 4. Left branch of portal vein.

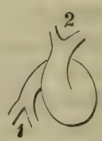
According to Guy, the umbilical vein is completely closed at the end of the fifth day after birth.

The Heart, and Ductus Arteriosus.—When the embryonic circulation is first established, the heart is a simple tubular canal (Fig. 309), receiving the veins at its lower extremity, and giving off the arterial trunks at its upper extremity. In the progress of growth, it soon becomes bent upon itself; so that the entrance of the veins and the exit of the arteries come to be placed more nearly upon the same horizontal level (Fig. 310); but the entrance of the veins (1) is behind and a little below, while the exit of the arteries (2) is in front and a little above. The heart is then a simple twisted tube; and the blood passes through it in a continuous stream, turning upon itself at the point of curvature, and emerging by the arterial orifice.

Fig. 309.

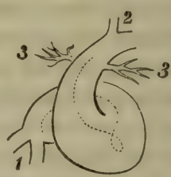
Earliest form of the Fœtal Heart.—1. Venous extremity. 2. Arterial extremity.

Fig. 310.



Fœtal Heart, bent upon itself.—1. Venous extremity. 2. Arterial extremity.

Fig. 311.

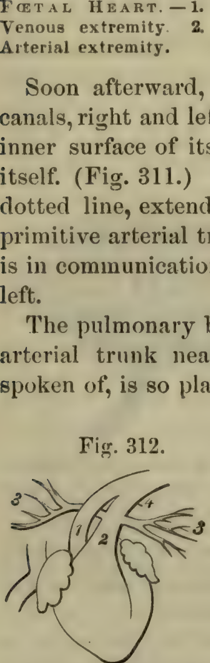


Fœtal Heart, divided into right and left cavities.—1. Venous extremity. 2. Arterial extremity. 3, 3. Pulmonary branches.

Soon afterward, the single cardiac tube is divided into two parallel canals, right and left, by a longitudinal partition, which grows from the inner surface of its walls and follows the twisted course of the organ itself. (Fig. 311.) This partition, which is indicated in the figure by a dotted line, extends a short distance into the commencement of the primitive arterial trunk, dividing it into two lateral halves, one of which is in communication with the right side of the heart, the other with the left.

The pulmonary branches (3, 3) are given off from each side of the arterial trunk near its origin; and the longitudinal partition, above spoken of, is so placed that both these branches fall upon one side of it, and are both, consequently, given off from that division of the artery which is connected with the right side of the heart.

Fig. 312.



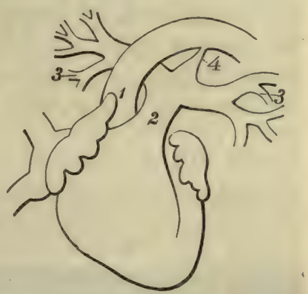
Fœtal Heart still farther developed.—1. Aorta. 2 Pulmonary artery. 3, 3. Pulmonary branches. 4. Ductus arteriosus.

The first portion of the arterial trunk is also divided into two parallel vessels of nearly similar curvature, which join each other a short distance beyond the origin of the pulmonary branches. The left lateral division of the arterial trunk is the commencement of the aorta (1); while its right lateral division is the trunk of the pulmonary artery (2), giving off the right and left pulmonary branches (3, 3), at a short distance from its origin. That portion of the

pulmonary trunk (4) which is beyond the origin of the pulmonary branches, and which communicates freely with the aorta, is the *Ductus arteriosus.*

The ductus arteriosus is at first as large as the pulmonary trunk itself; and nearly the whole of the blood coming from the right ventricle, passes through the arterial duct, and enters the aorta without going to the lungs. But as the lungs become developed, the pulmonary branches increase in proportion to the pulmonary trunk and to the ductus arteriosus. At the termination of fœtal life in man, the ductus arteriosus is about as large as either one of the pulmonary branches; and a considerable portion of the blood, therefore, coming from the right ventricle, still passes onward to the aorta without being distributed to the lungs.

Fig. 313.



HEART OF INFANT, showing the mode of disappearance of the arterial duct after birth.—1. Aorta. 2. Pulmonary artery. 3, 3. Pulmonary branches. 4. Ductus arteriosus becoming obliterated.

But at the period of birth, the lungs enter upon the performance of the function of respiration, and immediately require a greater supply of blood. The right and left pulmonary branches then enlarge, so as to become the two principal divisions of the pulmonary trunk. (Fig. 313.) The ductus arteriosus at the same time contracts to such an extent that its cavity is obliterated; and it is finally converted into an impervious cord, which remains until adult life, running from the point of bifurcation of the pulmonary artery to the under side of the arch of the aorta. The obliteration of the arterial duct is complete, at latest, by the tenth week after birth. (Guy.)

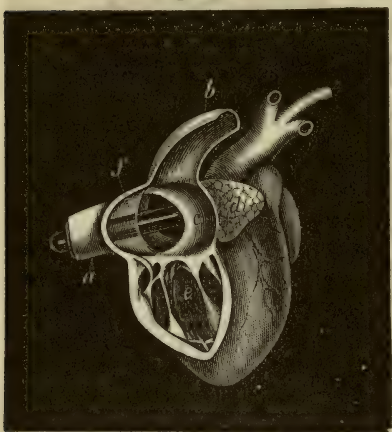
The two auricles are separated from the two ventricles by transverse septa which grow from the internal surface of the cardiac walls; but these septa remaining incomplete, the auriculo-ventricular orifices continue pervious, and allow the passage of the blood from the auricles to the ventricles.

The interventricular septum, or that which separates the two ventricles from each other, is completed at an early date; but the interauricular septum, or that situated between the two auricles, remains incomplete for a long time, being perforated by an oval-shaped opening, the *foramen ovale*, allowing, at this situation, a free passage from the right to the left side of the heart. The existence of the foramen ovale and of the ductus arteriosus gives rise to a peculiar crossing of the streams of blood in passing through the heart, which is characteristic of fœtal life, and which may be described as follows:

The two venæ cavæ in the fœtus do not open into the right auricle on the same plane or in the same direction; for while the superior vena cava is situated anteriorly, and is directed downward and forward, the

inferior is situated posteriorly, and passes into the auricle in a direction from right to left, transversely to the axis of the heart. A nearly vertical curtain or valve at the same time projects behind the orifice of the superior vena cava and in front of the orifice of the inferior. This curtain is formed by the lower and right hand edge of the septum of the auricles, which, as above mentioned, is incomplete at this time, and which terminates inferiorly and toward the right in a crescentic border, leaving an oval opening, the foramen ovale. The stream of blood, coming from the superior vena cava, falls in front of this curtain, and passes downward, through the auriculo-ventricular orifice, into the right ventricle. But the inferior vena cava, being farther back and directed transversely, opens, properly speaking, not into the right auricle, but into the left; for its stream of blood, falling behind the curtain above mentioned, passes across, through the foramen ovale, into the cavity of the left auricle. This direction of the current of blood, coming from the inferior vena cava, is further secured by a special membranous valve, which exists at this period, termed the *Eustachian valve.* This valve, which is very thin and transparent (Fig. 314, *f*), is attached to the anterior border of the orifice of the inferior vena cava, and terminates by a crescentic edge, directed toward the left; thus standing as an incomplete membranous partition between the cavity of the inferior vena cava and that of the right auricle. A bougie, placed in the inferior vena cava, as shown in Fig. 314, lies quite behind the Eustachian valve, and passes through the foramen ovale, into the left auricle.

Fig. 314.



Heart of the Human Fœtus, at the end of the sixth month; from a specimen in the author's possession.—*a.* Inferior vena cava. *b.* Superior vena cava. *c.* Cavity of the right auricle, laid open from the front. *d.* Appendix auricularis. *e.* Cavity of the right ventricle, also laid open. *f.* Eustachian valve. The bougie which is placed in the inferior vena cava, can be seen passing behind the Eustachian valve, just below the point indicated by *f*, then crossing behind the cavity of the right auricle, through the foramen ovale, to the left side of the heart.

The two streams of blood, therefore, coming from the superior and inferior venæ cavæ, cross each other upon entering the heart. This crossing does not take place in the cavity of the right auricle; but, owing to the position and direction of the two veins, the stream coming from the superior vena cava enters the right auricle, while that from the inferior passes almost directly into the left.

It also appears, from the relative position of the aorta, pulmonary artery, and ductus arteriosus, at this time, that the arteria innominata, together with the left carotid and left subclavian arteries, are given off

from the arch of the aorta, before its junction with the ductus arteriosus; and this arrangement causes the blood of the two venæ cavæ, not only to enter the heart in different directions, but also to be distributed, after leaving the ventricles, to different parts of the body. (Fig. 315.) The blood of the superior vena cava passes through the right auricle downward into the right ventricle, thence through the pulmonary artery and ductus arteriosus, into the thoracic aorta; while the blood of the inferior vena cava, entering the left auricle, passes into the left ventricle, thence into the arch of the aorta, and is distributed to the head and upper extremities. The two streams, therefore, in passing through the heart, cross each other both behind and in front. The venous blood, returning from the head and upper extremities by the superior vena cava, passes through the thoracic and abdominal aorta and the umbilical arteries, to the lower part of the body, and to the placenta; while that returning from the placenta, by the inferior vena cava, is distributed to the head and upper extremities, through the vessels given off from the arch of the aorta.

Fig. 315.

Diagram of the CIRCULATION THROUGH THE FŒTAL HEART.—*a.* Superior vena cava. *b.* Inferior vena cava. *c, c, c, c.* Arch of the aorta and its branches. *d.* Pulmonary artery.

This division of the streams of blood, during a certain period of fœtal life, is so complete that Reid,[1] on injecting the inferior vena cava with red, and the superior with yellow, in a human fœtus of seven months, found that the red injection had passed through the foramen ovale into the left auricle and ventricle and the arch of the aorta, and had filled the vessels of the head and upper extremities; while the yellow had passed into the right ventricle, pulmonary artery, ductus arteriosus, and thoracic aorta, with only a slight admixture of red at the posterior part of the right auricle. All the branches of the thoracic and abdominal aorta were filled with yellow, while the whole of the red had passed to the upper part of the body.

We have repeated this experiment several times on the fœtal pig, when about one-half and three-quarters grown, first taking the precaution to wash out the heart and large vessels with a watery injection, immediately after the removal of the fœtus, and before the blood had been allowed to coagulate. The injections used were blue for the superior vena cava, and yellow for the inferior. The two syringes were managed, at the same time, by the right and left hands; their nozzles being held in place by the fingers of an assistant. When the points of the syringes were introduced into the veins, at equal distances from the

[1] Edinburgh Medical and Surgical Journal, 1835, vol. xliii. p. 11.

heart, and the two injections made with equal rapidity, it was found that the admixture of the colors was so slight, that at least nineteen-twentieths of the yellow injection had passed into the left auricle, and nineteen-twentieths of the blue into the right. The pulmonary artery and ductus arteriosus contained a similar proportion of blue, and the arch of the aorta of yellow. In the thoracic and abdominal aorta, however, there was always an admixture of the two colors, generally in about equal proportions. This may be owing to the smaller size of the head and upper extremities in the pig, as compared with those of the human fœtus, which would prevent their receiving all the blood coming from the left ventricle; or to some difference in the manipulation of these experiments, in which it is not always easy to imitate exactly the force and rapidity of the different currents of blood in the living body. These results, however, leave no doubt of the fact, that, up to an advanced stage of fœtal life, by far the greater portion of the blood coming from the inferior vena cava passes through the foramen ovale, into the left side of the heart; while by far the greater portion of that coming from the head and upper extremities passes into the right side of the heart, and thence outward by the pulmonary trunk and ductus arteriosus. Toward the latter periods of gestation, this division of the venous currents becomes less complete, owing to the following causes.

First, the lungs increasing in size, the two pulmonary arteries, as well as the pulmonary veins, enlarge in proportion; and a greater quantity of the blood coming from the right ventricle, instead of going onward through the ductus arteriosus, passes to the lungs, and, returning thence by the pulmonary veins to the left auricle and ventricle, joins the stream passing out by the arch of the aorta.

Secondly, the Eustachian valve diminishes in size. This valve, which is very large at the end of the sixth month, subsequently becomes atrophied to such an extent that, at the end of gestation, it has either disappeared, or is reduced to the condition of a narrow membranous ridge, which can exert no influence on the current of the blood. Thus, the cavity of the inferior vena cava, at its upper extremity, ceases to be separated from that of the right auricle; and a passage of blood from one to the other may more readily take place.

Thirdly, the foramen ovale becomes partially closed by a valve which passes across its orifice from behind forward. This valve, which begins to be formed at a very early period, is the *valve of the foramen ovale.* It consists of a thin, fibrous sheet, which grows from the posterior surface of the auricular cavity, a little to the left of the foramen ovale, and projects into the left auricle, presenting a thin crescentic border, attached, by its two extremities, to the auricular septum upon the left side. The valve does not at first interfere with the flow of blood from right to left, since its edge hangs loosely into the cavity of the left auricle. It only opposes regurgitation from left to right.

But as gestation advances, while the walls of the heart continue to enlarge, and its cavities expand in every direction, the fibrous bundles,

forming the valve, do not elongate in proportion. The valve, accordingly, becomes drawn downward more closely toward the foramen ovale. It thus comes in contact with the edges of the inter-auricular septum, and unites with its substance; the adhesion taking place first at the lower and posterior portion, and proceeding gradually upward and forward, so that the passage from the right auricle to the left becomes constantly more oblique in direction.

At the same time there is an alteration in the position of the inferior vena cava. This vessel, which at first looked transversely toward the foramen ovale, becomes directed more obliquely forward; and thus, the Eustachian valve having nearly disappeared, a part of the blood of the inferior vena cava enters the right auricle, while the remainder still passes through the equally oblique opening of the foramen ovale.

At birth a change takes place, by which the foramen ovale is completely occluded, and all the blood coming through the inferior vena cava is turned into the right auricle.

The change depends upon the commencement of respiration. When this occurs, a much larger quantity of blood is sent to the lungs, and of course returns from them to the left auricle. The left auricle, being thus filled with blood from the lungs, no longer admits the entrance of a further quantity from the right auricle through the foramen ovale; and the valve of the foramen, pressed backward against the edges of the septum, becomes after a time adherent throughout, and thus obliterates the opening. The cutting off of the placental circulation diminishes at the same time the quantity of blood arriving at the heart by the inferior vena cava. It is evident that the same quantity of blood which previously returned from the placenta by the inferior vena cava on the right side of the inter-auricular septum, now returns from the lungs, by the pulmonary veins, upon the left side of the same septum; and it is owing to all these circumstances combined, that, while before birth a portion of the blood always passed from the right auricle to the left through the foramen ovale, no such passage takes place after birth, since the pressure is then equal on both sides of the auricular septum.

The fœtal circulation is then replaced by the adult circulation, represented in Fig. 316.

That portion of the inter-auricular septum, originally occupied by the foramen ovale, is accordingly constituted, in the adult condition, by the valve of the foramen ovale, which has become adherent to the edges of the septum. The septum in the adult heart is, therefore, thinner at this spot than elsewhere; and presents, on the side of the right auricle, an oval depression, termed the *fossa ovalis*, which indicates the site of the original foramen ovale. The fossa ovalis is surrounded by a slightly raised ring, the *annulus ovalis*, representing the curvilinear edge of the original inter-auricular septum.

The foramen ovale is sometimes completely obliterated within a few days after birth, but often remains partially pervious for several weeks

or months. We have a specimen, taken from a child one year and nine months old, in which the opening is still very distinct; and it is not unfrequent to find a small aperture existing even in adult life. In these

Fig. 316.

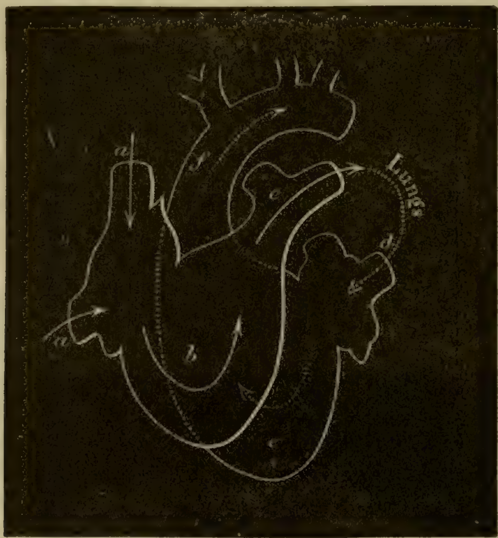


Diagram of the Adult Circulation through the Heart.—*a*, *a*. Superior and inferior venæ cavæ. *b*. Right ventricle. *c*. Pulmonary artery, dividing into right and left branches. *d*. Pulmonary vein. *e*. Left ventricle. *f*. Aorta.

instances, although the adhesion and solidification of the inter-auricular septum may not be complete, yet no admixture of blood takes place between the right and left sides of the heart; since the direction of the passage is always very oblique, and its valvular arrangement prevents any regurgitation from left to right. The complete filling of the left auricle with arterial blood, returning from the lungs, also opposes a complete obstacle to the entrance of venous blood from the right auricle.

CHAPTER XVIII.

DEVELOPMENT OF THE BODY AFTER BIRTH.

The newly-born infant is still far from having arrived at a state of complete development. The changes through which it has passed while in the fœtal condition are followed by others during the periods of infancy, childhood, and adolescence. The anatomy of the organs, both internal and external, their physiological functions, and even the morbid derangements to which they are subject, continue to undergo gradual and progressive alterations, throughout the entire course of subsequent life. The history of development extends, properly speaking, from the earliest organization of the embryonic tissues to the complete formation of the adult body. The period of birth marks only a single epoch in a constant series of changes, some of which have preceded, while many others are to follow.

The weight of the newly-born infant is about seven pounds. The middle point of the body is nearly at the umbilicus, the head and upper extremities being still large, in proportion to the lower extremities and the pelvis. The abdomen is larger and the chest smaller, in proportion, than in the adult. The lower extremities are still partially curved inward, so that the soles of the feet look obliquely toward each other, instead of being directed horizontally downward, as at a subsequent period. Both the arms and the legs are curled upward and forward over the chest and the abdomen, and all the joints are in a semi-flexed position.

The process of respiration is imperfectly performed for some time after birth. The expansion of the pulmonary vesicles, and the changes in the circulatory apparatus which take place at the time of birth, far from being instantaneous, are always more or less gradual in character, and require an interval of several days for their completion. Respiration seems to be accomplished, during this period, to a considerable extent through the skin, which is remarkably soft, vascular, and ruddy. The animal heat is less actively generated than in the adult, and requires to be sustained by careful protection, and by contact with the body of the mother. The young infant sleeps during the greater part of the time; and even when awake exhibits comparatively few manifestations of intelligence or perception. The special senses of sight and hearing are dull and inexcitable, and even consciousness seems present only to a limited extent. Voluntary motion and sensation are

nearly absent; and the almost constant irregular movements of the limbs, observable at this time, are mainly automatic. Nearly all the nervous phenomena presented by the newly-born infant, are of a similar nature. The motions of its hands and feet, the act of suckling, and even its cries and the contortions of its face, are reflex in their origin, and do not indicate the existence of active volition, or distinct perception of external objects. There is at first but little nervous connection with the external world, and the system is almost exclusively occupied with the functions of nutrition and respiration.

The difference in organization between the newly-born infant and the adult may be represented, to some extent, by the following list, which gives the relative weight of the most important internal organs at the period of birth and in adult age; the weight of the entire body being reckoned, in each case, as 1000. The relative weight of the adult organs has been calculated from the estimates of Cruveilhier, Solly, and Wilson, that of the organs in the fœtus at term from our own observations.

	Fœtus at term.	Adult.
Weight of the entire body	1000.00	1000.00
" " encephalon	148.00	23.00
" " liver	37.00	29.00
" " heart	7.77	4.17
" " kidneys	6.00	4.00
" " supra-renal capsules	1.63	0.13
" " thyroid gland	0.60	0.51
" " thymus gland	3.00	0.00

It appears that most of the internal organs diminish in relative size after birth, owing principally to the increased development of the osseous and muscular systems, both of which are in an imperfect condition throughout intra-uterine life, but come into activity during childhood and youth.

The remains of the umbilical cord begin to wither within the first day after birth, and become completely desiccated by about the third day. A superficial ulceration then takes place at the point of its attachment, and it is separated and thrown off within the first week. After the separation of the cord, the umbilicus becomes completely cicatrized by the tenth or twelfth day. (Guy.)

An exfoliation and renovation of the cuticle take place over the whole body soon after birth. According to Kölliker, the eyelashes, and probably all the hairs of the body and head, are thrown off and replaced by new ones within the first year.

The teeth in the newly-born infant are but partially developed, being still inclosed in their follicles and concealed beneath the gums. They are twenty in number, namely, two incisor, one canine, and two molar teeth on each side of each jaw. At birth there is a thin layer of dentine and enamel covering their upper surfaces, but the body of the tooth and its fangs are formed subsequently by progressive elongation and

ossification of the tooth-pulp. The fully-formed teeth emerge from the gums in the following order. The central incisors in the seventh month after birth; the lateral incisors in the eighth month; the anterior molars at the end of the first year; the canines at a year and a half; and the second molars at two years (Kölliker). The eruption of the teeth in the lower jaw generally precedes by a short time that of the corresponding teeth in the upper jaw.

During the seventh year a change begins to take place by which the first set of teeth are thrown off and replaced by the second or permanent set, which are different in number, size, and shape from the preceding. The anterior permanent molar tooth first shows itself just behind the posterior temporary molar, on each side. This happens at about six and a half years after birth. At the end of the seventh year the middle incisors are thrown off and replaced by corresponding permanent teeth, of larger size. At the eighth year a similar exchange takes place in the lateral incisors. In the ninth and tenth years, the anterior and second molars are replaced by the anterior and second permanent bicuspid teeth. In the twelfth year, the canine teeth are changed. In the thirteenth year the second permanent molars show themselves; and from the seventeenth to the twenty-first year, the third molars, or "wisdom teeth," emerge from the gums, at the posterior extremities of the dental arch. (Wilson.) The jaw, therefore, in the adult condition, contains three teeth on each side more than in childhood, making in all thirty-two permanent teeth; namely, on each side, above and below, two incisors, one canine, two bicuspids, and three permanent molars.

The generative apparatus, which is still inactive at birth, begins to enter upon a condition of functional activity from the fifteenth to the twentieth year. The entire configuration of the body alters at this period, and the distinction between the sexes becomes more marked. The beard is developed in the male; and in the female the breasts assume the size and form characteristic of the condition of puberty. The voice, which is shrill and sharp in infancy and childhood, becomes deeper in tone, and the countenance assumes a more sedate expression. After this period, the muscular system increases still further in size and strength, and the consolidation of the skeleton also continues; the bony union of its various parts not being entirely accomplished until the twenty-fifth or thirtieth year. Finally, all the different organs of the body arrive at the adult condition, and the entire process of development is then complete.

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